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# FIELDIANA

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## Botany

NEW SERIES, NO. 45

### FLORA COSTARICENSIS

William Burger, Editor

### Family #172 Ericaceae

James L. Luteyn  
Robert L. Wilbur

December 21, 2005  
Publication 1536

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Families of seed plants known or expected to occur in Costa Rica and adjacent areas, listed alphabetically and numbered according to the sequence of Engler's *Syllabus der Pflanzenfamilien*, edition 11, reworked by L. Diels (1936).

200	Acanthaceae	156	Elaeagnaceae	65	Nyctaginaceae
136	Actinidiaceae	130	Elaeocarpaceae	71	Nymphaeaceae
67	Aizoaceae	143	Elatinaceae	137	Ochnaceae
11	Alismataceae	172	Ericaceae	56	Oleaceae
64	Amaranthaceae	23	Eriocaulaceae	181	Oleaceae
30	Amaryllidaceae	102	Erythroxylaceae	164	Onagraceae
117	Anacardiaceae	113	Euphorbiaceae	57	Opiliaceae
77	Annonaceae	96	Fabaceae,	39	Orchidaceae
184	Apocynaceae		see Leguminosae	197	Orobanchaceae
119	Aquifoliaceae	50	Fagaceae	98	Oxalidaceae
19	Araceae	148	Flacourtiaceae	17	Palmae
166	Araliaceae	82	Fumariaceae,	82	Papaveraceae
4	Araucariaceae		see Papaveraceae	150	Passifloraceae
59	Aristolochiaceae	45	Garryaceae	195	Pedaliaceae
185	Asclepiadaceae	183	Gentianaceae	66	Phytolaceaceae
61	Balanophoraceae	99	Geraniaceae	5	Pinaceae
127	Balsaminaceae	198	Gesneriaceae	41	Piperaceae
69	Basellaceae	7	Gnetaceae	171	Pyrolaceae
48	Batidaceae	15	Gramineae	201	Plantaginaceae
153	Begoniaceae	142	Guttiferae	176	Plumbaginaceae
74	Berberidaceae	29	Haemodorumaceae	3	Podocarpaceae
49	Betulaceae	165	Halorrhagaceae	54	Podostemonaceae
194	Bignoniaceae	93	Hamamelidaceae	187	Polemoniaceae
145	Bixaceae	81	Hernandiaceae	111	Polygalaceae
133	Bombacaceae	124	Hippocastanaceae	62	Polygonaceae
189	Boraginaceae	121	Hippocrateaceae	26	Pontederiaceae
24	Bromeliaceae	101	Humiriaceae,	68	Portulacaceae
91	Brunelliaceae		see Linaceae	9	Potamogetonaceae
38	Burmanniaceae	60a	Hydnoraceae	175	Primulaceae
106	Burseraceae	13	Hydrocharitaceae	55	Proteaceae
12	Butomaceae	188	Hydrophyllaceae	158	Punicaceae
115	Buxaceae	142	Hypericaceae,	140	Quiinaceae
154	Cactaceae		see Guttiferae	60b	Rafflesiaceae
96	Caesalpinaceae,	122	Leguminosae	73	Ranunculaceae
	see Leguminosae	33	Iridaceae	86	Resedaceae
114	Callitrichaceae	47	Juglandaceae	128	Rhamnaceae
207	Campanulaceae	27	Juncaceae	160	Rhizophoraceae
36	Cannaceae	9	Kentziaceae	94	Rosaceae
83	Capparidaceae	9	Labiales	202	Rubiaceae
203	Caprifoliaceae	80	Lauraceae	104	Rutaceae
151	Caricaceae	159	Lecythidaceae	126	Sabiaceae
138	Caryocaraceae	96	Leguminosae	44	Salicaceae
70	Caryophyllaceae	20	Lemnaceae	125	Sapindaceae
40	Casuarinaceae	199	Lentibulariaceae	177	Sapotaceae
120	Celastraceae	28	Liliaceae	90	Saxifragaceae
72	Ceratophyllaceae	101	Linaceae	193	Scrophulariaceae
63	Chenopodiaceae	152	Loasaceae	105	Simarubaceae
42	Chloranthaceae	182	Loganiaceae	192	Solanaceae
144	Cistaceae	58	Loranthaceae	122	Staphyleaceae
169	Clethraceae	157	Lythraceae	134	Sterculiaceae
146	Cochlospermaceae	76	Magnoliaceae	180	Styracaceae
161	Combretaceae	108	Malpighiaceae	179	Symplocaceae
25	Commelinaceae	132	Malvaceae	2	Taxaceae
208	Compositae	37	Marantaceae	141	Theaceae
95	Connaraceae	139	Marcgraviaceae	173	Theophrastaceae
186	Convolvulaceae	196	Martyniaceae	155	Thymelaeaceae
116	Coriariaceae	21	Mayacaceae	131	Tiliaceae
168	Cornaceae	163	Melastomataceae	85	Tovariaceae
89	Crassulaceae	107	Meliaceae	109	Trigonaceae
84	Cruciferae	75	Menispermaceae	14	Triuridaceae
206	Cucurbitaceae	96	Mimosaceae,	100	Tropaeolaceae
92	Cunoniaceae		see Leguminosae	149	Turneraceae
6	Cupressaceae	79	Monimiaceae	8	Typhaceae
1	Cycadaceae	170	Monotropaceae	51	Ulmaceae
18	Cyclanthaceae	52	Moraceae	167	Umbelliferae
16	Cyperaceae	87	Moringaceae	53	Urticaceae
118	Cyrtillaceae	34	Musaceae	204	Valerianaceae
112	Dichapetalaceae	46	Myricaceae	31	Velloziaceae
135	Dilleniaceae	78	Myristicaceae	190	Verbenaceae
32	Dioscoreaceae	174	Myrsinaceae	147	Violaceae
205	Dipsacaceae	162	Myrtaceae	129	Vitaceae
88	Droseraceae	10	Najadaceae	110	Vochysiaceae
178	Ebenaceae			22	Xyridaceae
				35	Zingiberaceae
				103	Zygophyllaceae

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#### Family #172 Ericaceae

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## Abstract

A treatment of the 21 genera, 93 species, one subspecies, and four varieties of Ericaceae currently known from within the political borders of Costa Rica as well as those taxa currently known from the adjacent Chiriquí highlands of western Panama is herewith presented. Seventy-one of the 93 total species, the one subspecies, and three of the four varieties are found in Costa Rica, of

which 19 species, the one subspecies, and two of the four varieties are endemic there. The conservation status of each species is given based on 35 years of collecting experience and the numbers of herbarium specimens extant. Habitats, habits, field characters, keys, illustrations, and discussions of species relationships are given as aids to identification.

## Resumen

Se presenta un tratamiento de los 21 géneros, 93 especies, una subespecie y cuatro variedades de Ericaceae conocidos dentro del límite geográfico de Costa Rica, así como también los taxones de las tierras altas adyacentes a Chiriquí en la parte oeste de Panamá. Setenta y una de un total de 93 especies, la subespecie y tres de las cuatro variedades se encuentran en Costa Rica. De éstas, 19 especies, la subespecie y dos de las cuatro varie-

dades son endémicas allí. Se presenta el estado de conservación de cada especie basado en 35 años de experiencia colectando en el campo y en el número de muestras de herbario. Se dan hábitats, hábitos, características de la planta en el campo, claves, ilustraciones y discusiones sobre las relaciones entre las especies como guías para la identificación.

## Introduction

This is the twelfth issue in the *Flora Costaricensis* series. The first dealt with the Piperaceae, family number 41 (Fieldiana, Bot. 35, 1971). The second included families numbered 42 through 53, Chloranthaceae through Urticaceae (Fieldiana, Bot. 40, 1977). The third issue covered the Poaceae (Fieldiana, Bot. n.s. No. 4, 1980). The fourth issue included families numbered 54 through 70, Podostemaceae through Caryophyllaceae (Fieldiana, Bot. n.s. No. 13, 1983). The fifth issue covered families 200 and 201, the Acanthaceae and Plantaginaceae (Fieldiana, Bot. n.s. No. 18, 1986). The sixth issue included families 80 and 81, Lauraceae and Hernandiaceae (Fieldiana, Bot. n.s. No. 23, 1990). The seventh issue included families numbered 97 through 103, Krameriaceae through Zygophyllaceae (Fieldiana, Bot. n.s. No. 28, 1991). The eighth issue included family 202, the Rubiaceae (Fieldiana, Bot. n.s. No. 33, 1993). The ninth issue included family 113, the Euphorbiaceae (Fieldiana, Bot. n.s. No. 36, 1995). The tenth issue covered Tribe Maxillarieae of family 39, the Orchidaceae (Fieldiana,

Bot. n.s. No. 40, 1999). The eleventh issue included families numbered 193 through 197, Scrophulariaceae through Orobanchaceae (Fieldiana, Bot. n.s. No. 41, 2000).

In keeping with the original intent of *Flora Costaricensis* and for the biogeographical reasons discussed here, this treatment of Ericaceae includes both those taxa currently known from within the political borders of Costa Rica as well as those taxa currently known from the adjacent Chiriquí highlands of western Panama. Many of the species here described and discussed are illustrated by means of color photos on Luteyn's Web site given in the "References" section below.

In Figures 3–15, leaves and leafy stems are drawn to the same scale throughout. Enlarged flowers and fruits are drawn to the same scale on an individual plate unless otherwise noted. The closed scales represent centimeters, and the open scales represent millimeters. The figures are somewhat diagrammatic and represent the artist's (William Burger) concept of a common or characteristic morphology.

## Acknowledgments

The authors wish to express our grateful acknowledgment to the National Science Foundation, whose support over the years made this study possible. J.L.L. wishes to thank The Field Museum of Natural History (Chicago) for financial aid from the Robert O. Bass Visiting Scientist Fund that enabled him to work at the Field Museum. Obviously a study such as the present one would be impossible without the cooperation of the curators of the many herbaria who loaned their collections for this investigation. We are very much indebted to the curatorial staff of the following herbaria: A, AAU, BM, CAS, CR, CU, DAV, DS, DUKE, F, GB, GH, INB, K, L, LL, MICH, MIN, MO, MSC, NY, P, PH, PMA, POM, RSA, S, SCZ, TEX, US, WIS. We wish to thank the Museo Nacional de Costa Rica, the Instituto

Nacional de Biodiversidad (INBIO), the Field Museum of Natural History (Chicago), and the Missouri Botanical Garden for their assistance in local collecting programs and their staff and facilities over the many years the writing of the manuscript has spanned. Bill Haber and Willow Zuchowski provided logistical support to J.L.L. during trips to Monteverde. For encouragement, profitable discussions, and the artistic talents of Bill Burger, which have helped greatly to embellish this work, we are grateful. Lucia Kawasaki helped in various aspects of the manuscript and logistically. Reviewer's comments on the manuscript are appreciated. J.L.L. wishes to thank the Missouri Botanical Garden for providing facilities to complete this manuscript. Bobbi Angell's plates (Figs. 1–2) are beautiful, as always.

# FLORA COSTARICENSIS

## Family #172 Ericaceae

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### ERICACEAE

By James L. Luteyn and  
Robert L. Wilbur

REFERENCES—K. A. Kron, W. S. Judd, P. F. Stevens, D. M. Crayn, A. A. Anderberg, P. A. Gadek, C. J. Quinn, & J. L. Luteyn, Phylogenetic classification of Ericaceae: Molecular and morphological evidence. *Bot. Rev.* 68: 335–423. 2002. J. L. Luteyn, Key to the subfamilies and genera of neotropical Ericaceae. *Nord. J. Bot.* 11: 623–627. 1991. J. L. Luteyn, Ericaceae, in G. Harling & L. Andersson (eds.), *Flora of Ecuador* 54: 1–404, I–VIII. 1996. J. L. Luteyn, “Neotropical blueberries: The plant family Ericaceae.” <http://www.nybg.org/bot/res/lut2>. 1998. J. L. Luteyn, Diversity, adaptation, and endemism in Neotropical Ericaceae: Biogeographical patterns in the Vaccinieae. *Bot. Rev.* 68: 55–87. 2002. J. L. Luteyn & R. L. Wilbur, Ericaceae, in *Flora of Nicaragua* 1: 822–831. 2002. P. C. Standley & L. O. Williams, Ericales, in *Flora of Guatemala*. Fieldiana, Bot. 24 (pt. 8): 73–127. 1966. P. F. Stevens, J. L. Luteyn, et al., Ericaceae, in K. Kubitski (ed.), *Families of Flowering Plants*, vol. VI: 145–194. 2004. R. L. Wilbur & J. L. Luteyn, Ericaceae, in R. Woodson et al., *Flora of Panama*. *Ann. Missouri Bot. Gard.* 65: 27–144. 1978.

Terrestrial or epiphytic **shrubs**, **subshrubs**, perennial **herbs**, or fleshy achlorophyllous mycotrophs (*Monotropa*), sometimes lianoid or rarely **trees**, often rhizomatous, sometimes arising from lignotubers (spherical to oblong, swollen hypocotyls, 0.4–1 m diam., little vascular tissue, mostly parenchyma); **indumentum** mostly of simple, unicellular hairs, also with stout, multicellular, multiserial, usually glandular, brownish-red, clavate to capitate hairs (these sometimes fusing as fimbriae, then occurring on mature stems, leaves, or pedicels and the organ referred to as fimbriate); apical bud usually aborting, especially in Vaccinioideae; axillary buds scaly (outer pair elongated and rarely appearing stipular). **Leaves** alternate (usually spiral, rarely distichous), rarely (our species) opposite or pseudo-opposite, verticillate,

whorled (pseudo-whorled in *Chimaphila*), or reduced and then represented by bract-like scales (*Monotropa*), simple, usually petiolate, exstipulate, the blade coriaceous to membranous, evergreen to deciduous, the margin usually entire but sometimes serrulate-crenate, the venation plinerved (with a clear midrib and several strong lateral nerves) or pinnate; leaf scars with a single vascular bundle scar, the nodes with one trace and one gap (our species). **Inflorescences** axillary, rarely terminal, racemose, paniculate, fasciculate, or flowers solitary; floral bract 1, subtending pedicel of each flower, small or large, showy or inconspicuous, deciduous or persistent; pedicels articulate or continuous with calyx; bracteoles usually 2, usually smaller than floral bracts, borne along length of each pedicel. **Flowers** bisexual (rarely functionally unisexual; plants dioecious in some species of *Pernettya* in temperate South America), radially symmetrical or slightly bilaterally symmetrical, mostly (3) 5 (7)-merous, typically obdiplostemonous, hypogynous, or epigynous and with a typically biseriate perianth; calyx synsepalous at least basally, in superior ovaries the sepals are distinct or almost distinct, imbricate, sometimes grading into bract-like scales (*Monotropa*), rarely fleshy and accrescent to the fruit (*Gaultheria*), in inferior ovaries the proximal (or inferior) part of the calyx that is fused with the ovary wall is called the “calyx tube” (previous Luteyn papers often called this part the hypanthium), which is basally rounded to truncate or sometimes outwardly flaring and then said to be apophysate, the distal free part (of the calyx) that is borne on top of the ovary is the “calyx limb,” and the portions of the limb that are distinct from one another are the “calyx lobes”; **corolla** sympetalous, lobed, aestivation imbricate or valvate, membranous to carnosous, unistratose or bistratose, commonly cylindric, campanulate or urceolate (petals distinct in *Bejaria*, *Monotropa*); **stamens** (see Figs. 1–2) (6) 10 (14), in 2 whorls, equaling to shorter than corolla overall, equal or alternately unequal within themselves, twice as many as the petals (rarely as many), arising from base of ovary and then sometimes alternating with lobes of nectaries (superior-ovary genera), or borne on edge of a nectariferous disc (inferior-ovary genera); filaments equal or alternately unequal, distinct or connate, usually straight (rarely slightly S-shaped), ligulate (sometimes broadened and papillose at base); connectives short and inconspicuous in superior-ovary genera, or thick and raised in inferior-ovary genera, bearing white, disintegration tissue powder in small, elongated pouches along length and onto awns (*Comarostaphylis*, *Gaultheria*, *Pernettya*), sometimes spurred (*Comarostaphylis*, *Psammisia*, *Vaccinium*); anthers inverting during development, the thecae oblong, bilocular, basally rounded or apiculate, sometimes bearing terminal awns (*Gaultheria*, *Pernettya*), in the superior-ovary genera thecae dehiscent

terminally or by obliquely introrse pores (*Bejaria*, *Gaultheria*, *Pernettya*), or longitudinally (*Monotropa*), in all the inferior-ovary genera each theca narrows apically into a hollow tubule through which pollen escapes, the tubules distinct or connate and dehiscing introrsely or rarely latrorsely by oblique pores or short to elongate clefts; pollen grains in tetrahedral tetrads (rarely single in *Monotropa*), sometimes with viscin threads (*Bejaria*); **pistil** single, the ovary superior or inferior, 4–5 (10)-carpellate, usually with as many locules as carpels or with twice as many locules as carpels (rarely loculate in lower portion and 1-locular above); placentation axile (rarely intruded parietal); ovules numerous (rarely solitary), anatropous to campylotropous with a single integumentary layer; style usually arising from a slight depression, single, fluted, hollow; stigma simple (occasionally weakly lobed in *Monotropa*); nectary present at base of ovary in superior-ovary genera and obscure (*Gaultheria*, *Pernettya*), or as 5 (*Chimaphila*) or 8–10 lobes (*Monotropa*) projecting from between filament bases, or as a continuous annular or cup-shaped disc covering entire top of ovary in inferior-ovary genera. **Fruit** loculicidal or septicidal capsules, berries, or drupes, with a usually persistent, rarely accrescent and fleshy calyx (*Gaultheria*); **seeds** small, usually numerous, sometimes winged or tailed (*Bejaria*, *Chimaphila*), sometimes covered by clear, mucilaginous sheath; testa thin with elongated or isodiametric cells; endosperm fleshy; embryo straight, white or sometimes green (*Sphrospermum*, *Themistoclesia*).

Ericaceae s.l. include about 125 genera and 4500 species worldwide. Except for Antarctica, the family is cosmopolitan, inhabiting temperate regions of the world and montane areas in tropical latitudes (Luteyn, 2002). Concentrations of high species diversity occur in the tropics of both hemispheres, the Himalayas, Australia, and the Cape Region of South Africa (Kron & Luteyn, 2005). In the Neotropics, overall species richness increases near the Equator, with the highest numbers in Colombia (ca. 300 spp.) and Ecuador (ca. 230 spp.). Forty-seven genera (ca. 70% endemic) and approximately 900 species (ca. 95% endemic) are native to the Neotropics. In this floristic treatment of Ericaceae for Costa Rica, we include a total of 21 genera with a total of 93 species, one subspecies, and four varieties. Seventy-one of the 93 total species, the one subspecies, and three of the four varieties are found in Costa Rica. Nineteen of those 93 species, along with the one subspecies and two of the four varieties, are currently endemic to Costa Rica. Another 22 species and one variety (including *Bejaria aestuans* and *Orthaea panamensis*) have yet to be found within the political boundaries of Costa Rica, although they **do** occur in the adjacent Chiriquí highlands of western Panama. We do not apologize for including this seemingly large number of “yet to be

discovered” taxa in this treatment of the Ericaceae of Costa Rica because similar life zones and habitats are present there, and, perhaps more importantly, the Caribbean slopes of the Cordillera de Talamanca are so poorly known botanically. In recent years, at least 23 species of Ericaceae, previously thought to be endemic to either Costa Rica or the western Chiriquí highlands of Panama, have now been collected in western Panama or eastern Costa Rica, respectively (13 species from the Costa Rican Talamancas are now found in the adjacent western Chiriquí highlands; 10 species from the western Chiriquí highlands are now found in the eastern Costa Rica Talamancas). Furthermore, geologically, the western highlands of Panama, including the uplands of Bocas del Toro and Chiriquí Provinces, and parts of the newly established Comarca Ngöbe-Buglé (formerly the Caribbean slopes of eastern Chiriquí Prov.), represent the easternmost extension of the Cordillera de Talamanca, which originates in central Costa Rica. At the same time, the western highlands of Panama represent the easternmost distribution point for many plant species in Mesoamerica. Therefore, we anticipate that most, if not all, of these additional 23 taxa actually occur in eastern Costa Rica and that more intensive botanical exploration on the Caribbean slopes of the Talamancas will reveal them. Two species of *Satyria* included within this treatment (*Satyria* sp. “A” and “B”) are considered as “morpho” species and have yet to be formally described. *Rhododendron simsii*, a native to China and sometimes encountered as a cultivated plant at higher elevations, is keyed but not described.

The family Ericaceae is economically important in temperate regions of the world, primarily for those genera of horticultural (*Erica*, *Rhododendron*) and commercial food crop (*Vaccinium*) usage. In the Neotropics, fruits of *Vaccinium floribundum* and *Macleania rupestris* are rarely found in local and commercial markets, although they are used in pies, jams, and drinks.

Ecologically, the Ericaceae are usually found in the moist habitats of cool montane forests between 1000 m and 3000 m elevation; in well-drained, acid soils; and where there is ample light and abundant, regularly distributed precipitation throughout the year—habitats that are also some of the most threatened ecosystems in the world (Mast et al., 1999; Knapp, 2002). They are often associated with mycorrhizal fungi and are frequently found as pioneers following volcanic, landslide, or road-building activities or as part of



the edge community around mature forests (Luteyn, 2002). The evergreen, coriaceous leaves of many Ericaceae provide an excellent substrate for mosses, hepatics, lichens, and other fungi. Also, glands and glandular areas on the mature stems, leaf surfaces, and inflorescences are often covered by fungal mycelia that probably derive nutrients from the exudates.

Pollination is typically by bees in the superior-ovary genera and by hummingbirds in the inferior-ovary genera. The floral morphology of the inferior-ovary genera, the "blueberries," indicates that many have a close evolutionary relationship with hummingbirds (Luteyn, 1998; Luteyn & Sylva S., 1999). Corollas of the blueberries house tiny, translucent mites (<1 mm long) of the genus *Rhioseius*, which breed and feed in the flowers and are dispersed in the nasal cavities of hummingbirds (Colwell, 1973, 1985; Nasrecki & Colwell, 1998). In the Neotropics, the berry fruits and abundant sugar-rich nectar provide sources of food for many animals. The two most important dispersal agents of Ericaceae at Monteverde (Costa Rica) include the Emerald Toucanets and Black-faced Solitaires (G. Murray, pers. comm.).

Based on a combination of morphological and molecular data, the families Monotropaceae and Pyrolaceae (both in Costa Rica) and Empetraceae and Epacridaceae recognized as distinct by Takhtajan (1980), Cronquist (1981), and others are now included within the Ericaceae sensu lato (see Anderberg, 1992, 1993; Judd & Kron, 1993; Kron & Chase, 1993; Kron, 1996; Kron et al., 2002a; Powell & Kron, 2003; and Stevens et al., 2004 for data and detailed discussions). However, generic limits in the tribe Vaccinieae are still poorly understood (Luteyn & Wilbur, 1997; Luteyn, 2001; Kron et al., 2002a,b).

The family is still revealing new species and new records for Costa Rica with many collecting efforts yielding novelties, emphasizing large gaps yet to be filled in our knowledge of neotropical families in general and of the floristic composition of this region. Contrary to some recent views that fieldwork in comparatively well-collected countries such as Costa Rica and Panama is no longer necessary, this treatment points out once again the absolute need for field collecting and basic herbarium research. Furthermore, in view of the well-publicized destruction of the rain forest, it also demonstrates the need for continued field work in montane as well as lowland regions. Inventory work at the primary level followed by revisionary

and monographic studies by specialists is still desperately needed, and actually its support must increase if we are to claim a true knowledge of tropical ecosystems. In an effort to alert scientists and the general public as to the conservation status of the Ericaceae in Costa Rica and the adjacent highlands of western Chiriquí Province, Panama, we have given our own personal assessment of each species herein treated based on each of our approximate 35 years of collecting experience in Costa Rica and Panama, combined with the numbers of herbarium specimens extant. The following five status categories are recognized: **Endangered** = species known from six or fewer collections or only a few localities that are threatened by human intervention; **Rare/Infrequent** = species known from 7–12 collections but in only a few, scattered localities; **Locally Common** = species known from more than 12 collections but in only a few, scattered localities; **Widespread** = species known from many geographic localities but few collections; **Common** = species known from many collections and many geographic localities.

In Costa Rica and adjacent western Panama, Ericaceae are relatively easily recognized by the following field characters: generally woody, sun-loving **shrubs**, whether terrestrial or epiphytic; **leaves** are spiral, lacking stipules, with blades that are usually thin and red when young but coriaceous and dark green when mature, the leaf venation is often strongly plinerved, the leaf margins are usually entire; **nodes** are unilacunar with one gap and one trace (use 10× lens); **indumentum** is rarely conspicuous; **inflorescences** are axillary but often appear terminal, the flowers are found in racemes, fascicles or are solitary, the pedicels are bibracteolate and articulate or continuous with the calyx; **flowers** are pendulous, perfect, actinomorphic, usually 4- to 5-merous, odorless; **calyx** has the sepals usually connate and persistent; **corolla** is often fleshy, usually of united petals, typically urceolate, cylindrical or sometimes campanulate, often waxy and nitid, often with the refreshing taste of oxalic acid (at least in the inferior-ovary genera), the colors of the corolla proper often contrast with those of the lobes or floral bracts; **stamens** are usually twice as many as the petals and free from them, the anthers are sometimes abaxially appendaged with awns or spurs and dehisce by apical pores or clefts often on the ends of long narrow tubules; **nectar** is usually abundant, sweet and viscid in the base of the corolla; **ovary** is superior or inferior with axile

placentation, the ovules are usually many per carpel, the style is hollow and usually impressed into the ovary, the stigma is truncate; **fruits** are brown and woody capsules, blue-black or rarely translucent white berries, or rarely blue-black drupes, the seeds are small, numerous and golden in color while the embryo is white or less commonly green.

In general, it is easy to find Ericaceae in Costa Rica. In cool, moist, montane regions they are good pioneers and opportunists, so the best places to find them are along roadside slopes, forest edges, and in remnant trees in pasturelands. Newly exposed land, whether due to man-made operations such as road building or forest clearing, or natural events such as volcanic activity, landslides, or tree falls, all provide Ericaceae with open to partially shaded, sparsely inhabited sites, where pollinating vectors (bees, hummingbirds) also have easy access. In terrestrial situations such as these, the shrubby plants often dominate and flourish for many years until they become overgrown, at which time they disappear or persist in lower numbers without flowering, having been literally shaded out or outcompeted by more aggressive vegetation. Their vitality is periodically renewed after road crews cut back the dense vegetation along road banks, thus again providing necessary sunlight for growth and flowering. A beautiful example of this situation may be seen along the interamerican highway above Cartago, where starting at about 1200 m the showy red and white flowers and bracts of *Cavendishia bracteata* are found and then, at a little higher elevation, populations of *Macleania rupestris* present a spectacular floral display among roadside bank vegetation. Also, a more natural and historic example of this terrestrial situation may be seen at the summit of Volcán Irazú, where three species of Ericaceae (*Comarostaphylis arbutoides*, *Pernettya prostrata*, *Vaccinium consanguineum*) were among the first pioneers to reestablish vegetation there after an eruption in 1963; by 1970 they were dominant. In epiphytic situations, newly exposed sites are often provided by forest clearing or tree falls, thus providing the required amount of sunlight to lower branches or remnant trees for ericads to grow and flower. It should be emphasized here that epiphytic Ericaceae are not common within a low-light forest or on young branches of the canopy, but instead they prefer exposed to partially shaded situations on older and larger branches with usually rough bark. Also, in low-light situations within the forest, they

usually become lianoid and do not flower. Both natural and disturbed open sites may be dry because of increased exposure and strong winds, and here Ericaceae may supplement their moisture needs by rooting in waterlogged rotting tree stumps like remnant trees in pasturelands or in dense and water-retaining bryophyte layers; water-storing lignotubers are also quite common (for additional explanation and examples, see Luteyn, 2002).

It is interesting that recent collecting activities, especially those made under the auspices of the INBIO biodiversity of Costa Rica program, have uncovered many new species or new records of Ericaceae in "lowland" (not montane) habitats below 700 m elevation. These include *Cavendishia herrerae*, *C. limonensis*, *C. linearifolia*, *C. osaensis*, *Didonica pendula*, *Satyria* species "A," *Sphyrrosperrum ellipticum*, and *Vaccinium furfuraceum*. This strongly suggests that there may be more species to be found in the wet, lowland rain forest and that our traditional characterization of this family as montane may need to be revised.

Although many of the commonly encountered Costa Rican Ericaceae have large and showy flowers to 2–3 cm long (e.g., *Cavendishia bracteata*, *Macleania rupestris*, *Psammisia ramiflora*, *Satyria warszewiczii*) or large floral bracts to 4 cm long with contrasting colors (e.g., *Cavendishia atrovioleacea*, *C. bracteata*, *C. callista*, etc.), quite a few also have small and inconspicuous flowers with minute, green, floral bracts and are therefore poorly collected (e.g., *Themistoclesia* spp.). Others occur as epiphytes high in old trees (e.g., *Themistoclesia pentandra* and *Uteleya costaricensis*). One plant, *Disterigma utleyorum*, may be rarely collected because of its association with aggressive, biting ants. The mycotrophic *Monotropa uniflora* and herbaceous subshrub *Chimaphila maculata* are easily overlooked in the forest understory under the best of conditions but are now rare and almost certainly endangered because their oak forest habitat is nearly completely destroyed in areas accessible to humans. A few species are rarely collected not only because they are truly very local and therefore rare in their occurrence but also because quite a few have small, green flowers (e.g., *Anthopterus costaricensis* and *A. revolutus*, *Didonica pendula*, *Lateropora ovata*, *Themistoclesia costaricensis* and *T. horquetensis*, *Vaccinium costaricense*, *V. floccosum*, *V. orosiense*, and *V. poasanum*). *Sphyrrosperrum dissimile*, on the other hand, is infrequently collected because it has small, dark brick-red corollas that

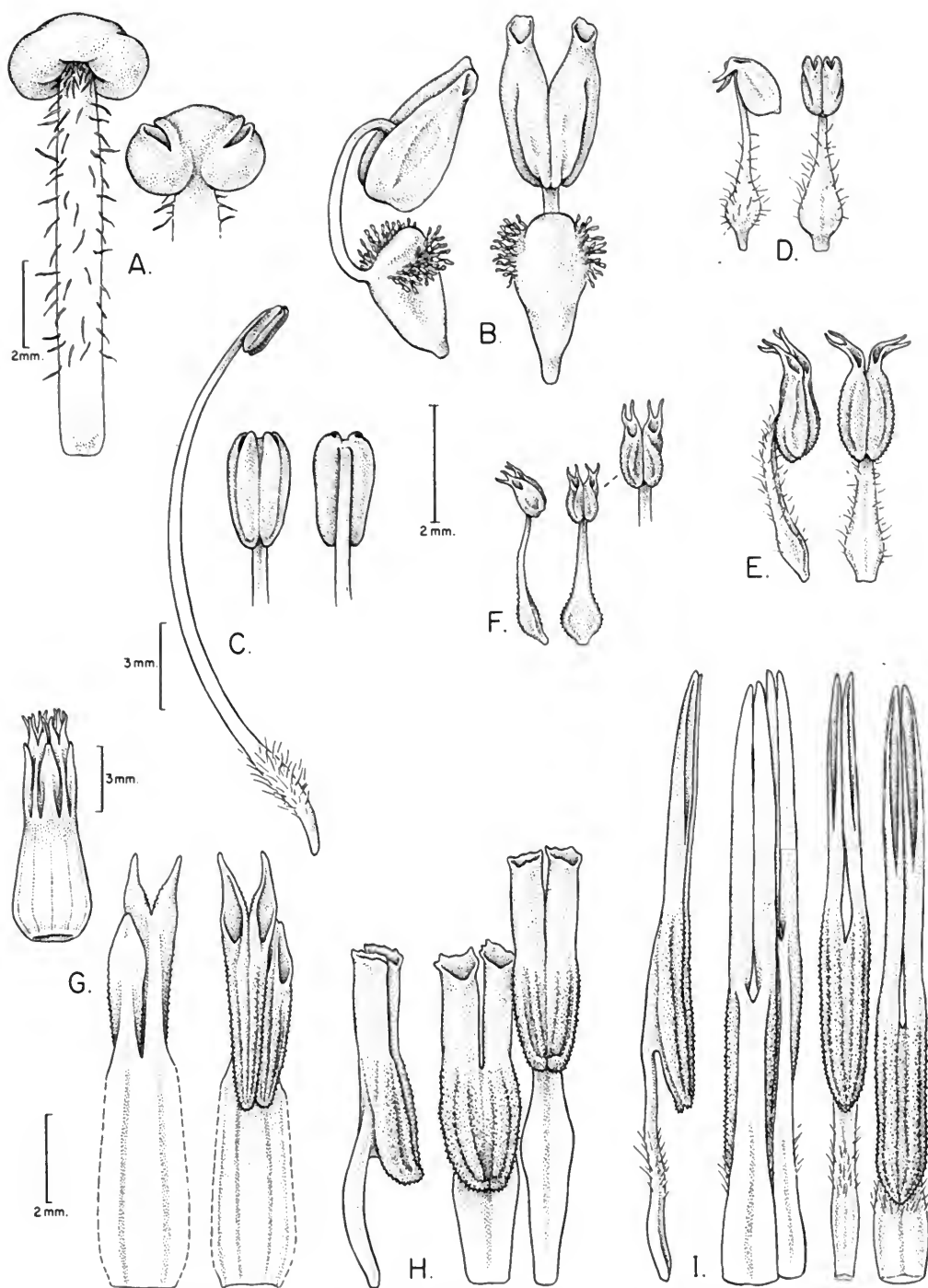


FIG. 1. Stamens from the genera of Costa Rican Ericaceae. (A) *Monotropa uniflora* (Luteyn et al. 11685, NY). (B) *Chinaphila maculata* (Davidse 25713, NY). (C) *Bejaria aestuans* (Luteyn & Lebrón-Luteyn 11415, NY). (D) *Comarostaphylis* (drawn from *C. discolor* subsp. *discolor*, Luteyn et al. 11616, NY). (E) *Gaultheria erecta* (Luteyn et al. 11607, NY). (F) *Pernettya prostrata* (Luteyn et al. 7389, NY). (G) *Satyria panurensis* (Luteyn et al. 15247, NY). (H) *Orthaea panamensis* (Luteyn 14863, NY). (I) *Cavendishia fortuneensis* (Luteyn 14824, NY). (Illustrations by Bobbi Angell)

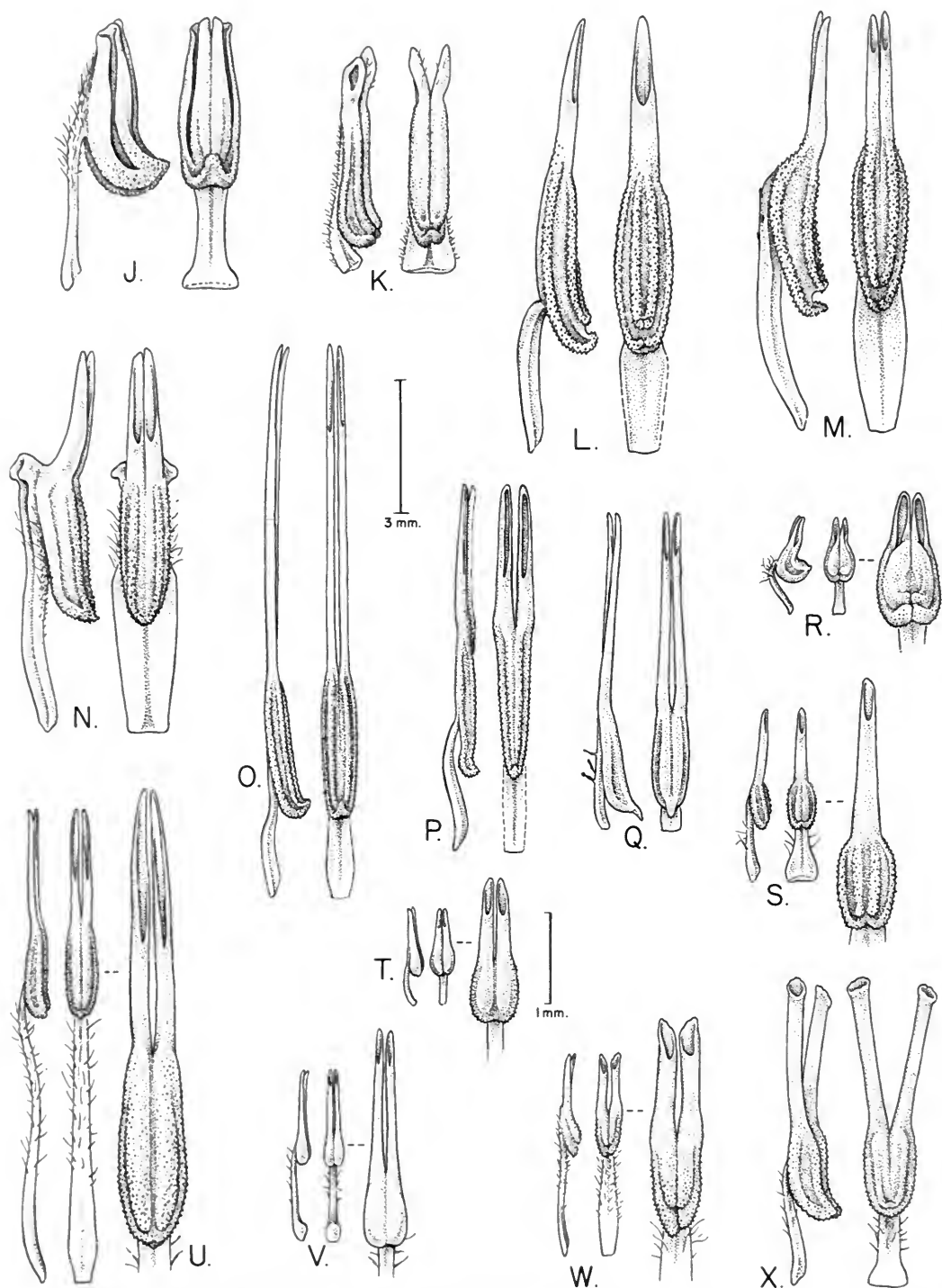


FIG. 2. Stamens from the genera of Costa Rican Ericaceae. (J) *Lateropora ovata* (Luteyn 14810, NY). (K) *Didonica pendula* (redrawn from Brittonia 29: 255, fig. 1. 1977). (L) *Macleania insignis* (Luteyn et al. 15240, NY). (M) *Macleania rupestris* (spirit material ex Longwood Gardens). (N) *Psanmisia ramiflora* (Luteyn et al. 15215, NY). (O) *Gonocalyx pterocarpus* (Luteyn et al. 15229, NY). (P) *Thibaudia costaricensis* (Luteyn 4531, NY). (Q) *Anthopteris revolutus* (Luteyn 14806, NY). (R) *Utleia costaricensis* (Luteyn et al. 4412, NY). (S) *Themistoclesia pentandra* (Luteyn 14862, NY). (T) *Themistoclesia smithiana* (Luteyn et al. 15249, NY). (U) *Disterigma humboldtii* (Luteyn & Pedraza 15573, NY). (V) *Sphyrsperrum cordifolium* (Luteyn et al. 15152, NY). (W) *Vaccinium consanguineum* (Luteyn et al. 15222, NY). (X) *Vaccinium poasanum* (Luteyn et al. 15219, NY). (Illustrations by Bobbi Angell)

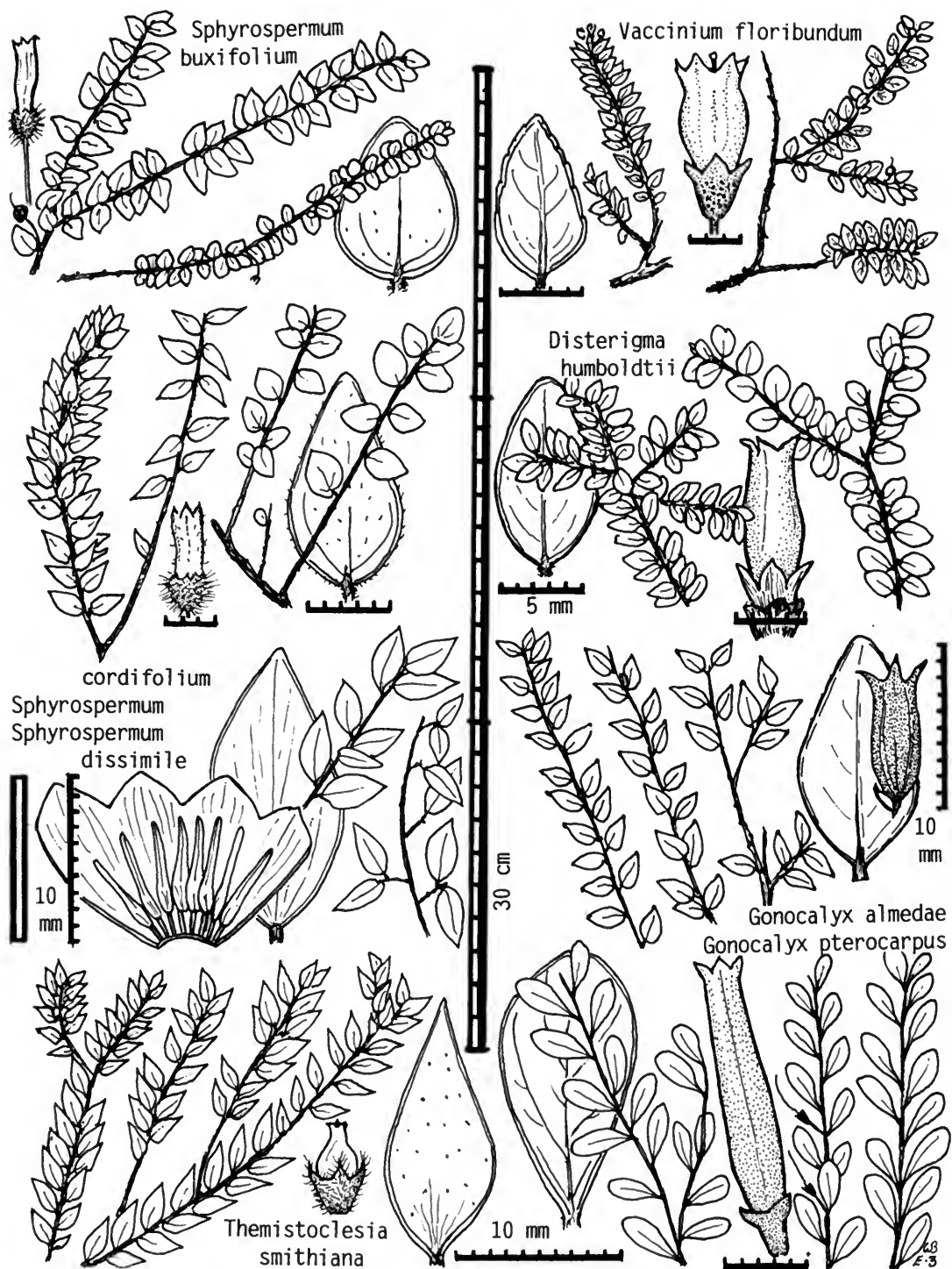


FIG. 3. Ericaceae shrubs with very small leaves: species of *Gonocalyx*, *Sphyrnospermum*, *Themistoclesia*, and *Vaccinium*.

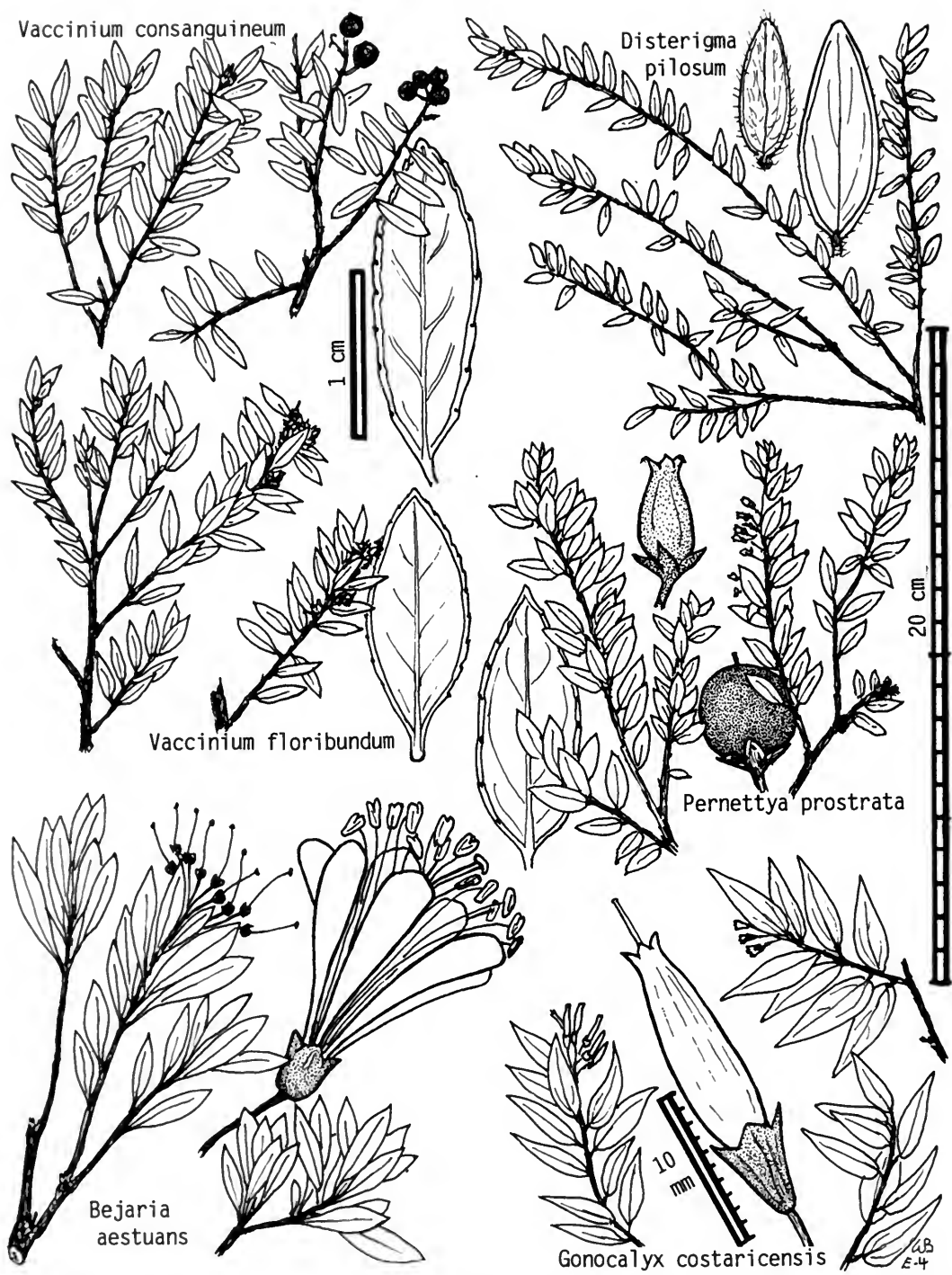


FIG. 4. Ericaceae shrubs with small, mostly narrow leaves: species of *Bejaria*, *Disterigma*, *Gonocalyx*, *Pernettya*, and *Vaccinium*.

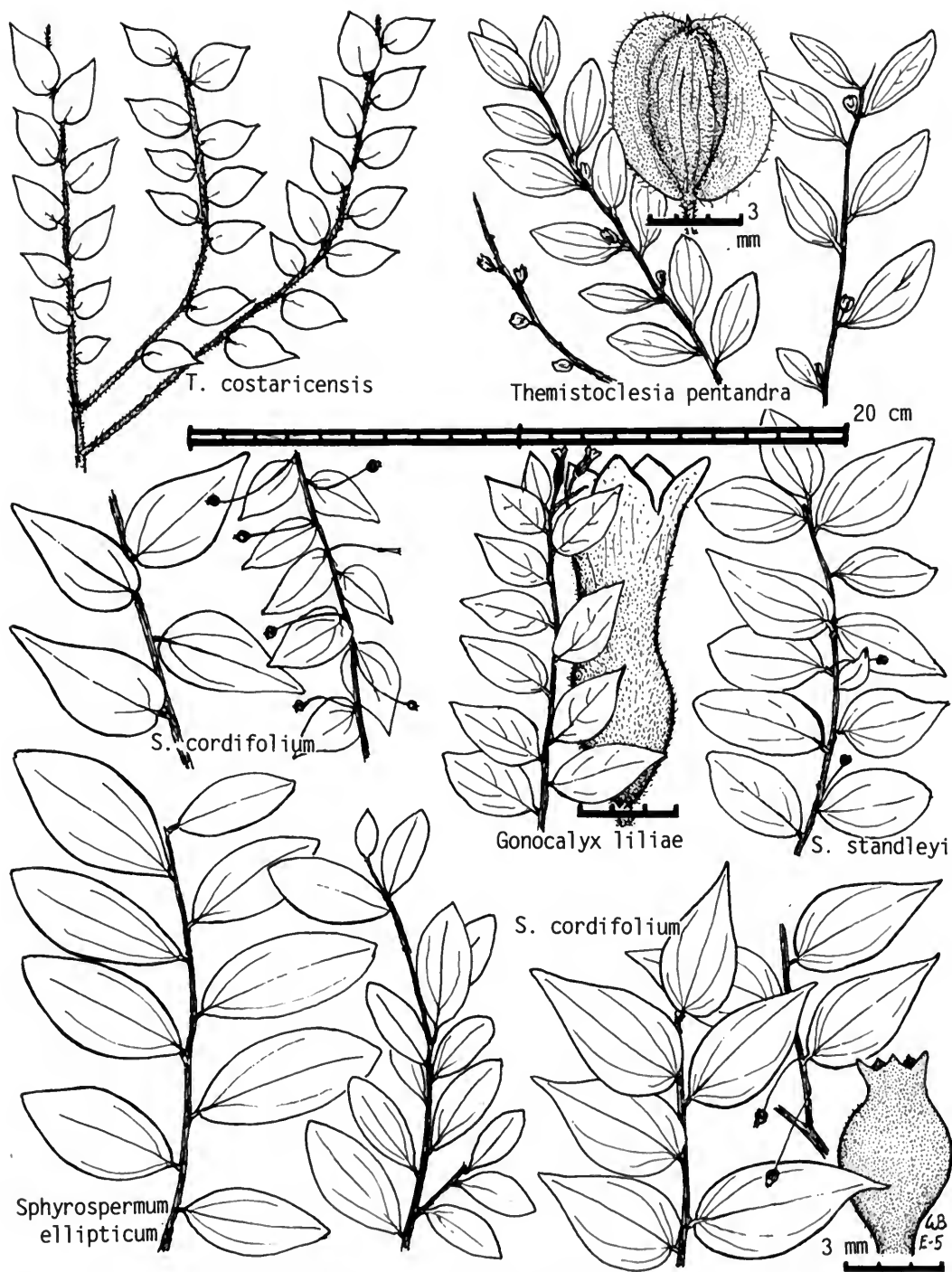


FIG. 5. Ericaceae shrubs with smaller, mostly ovate leaves: species of *Gonocalyx*, *Sphyrrosperrum*, and *Themistoclesia*.



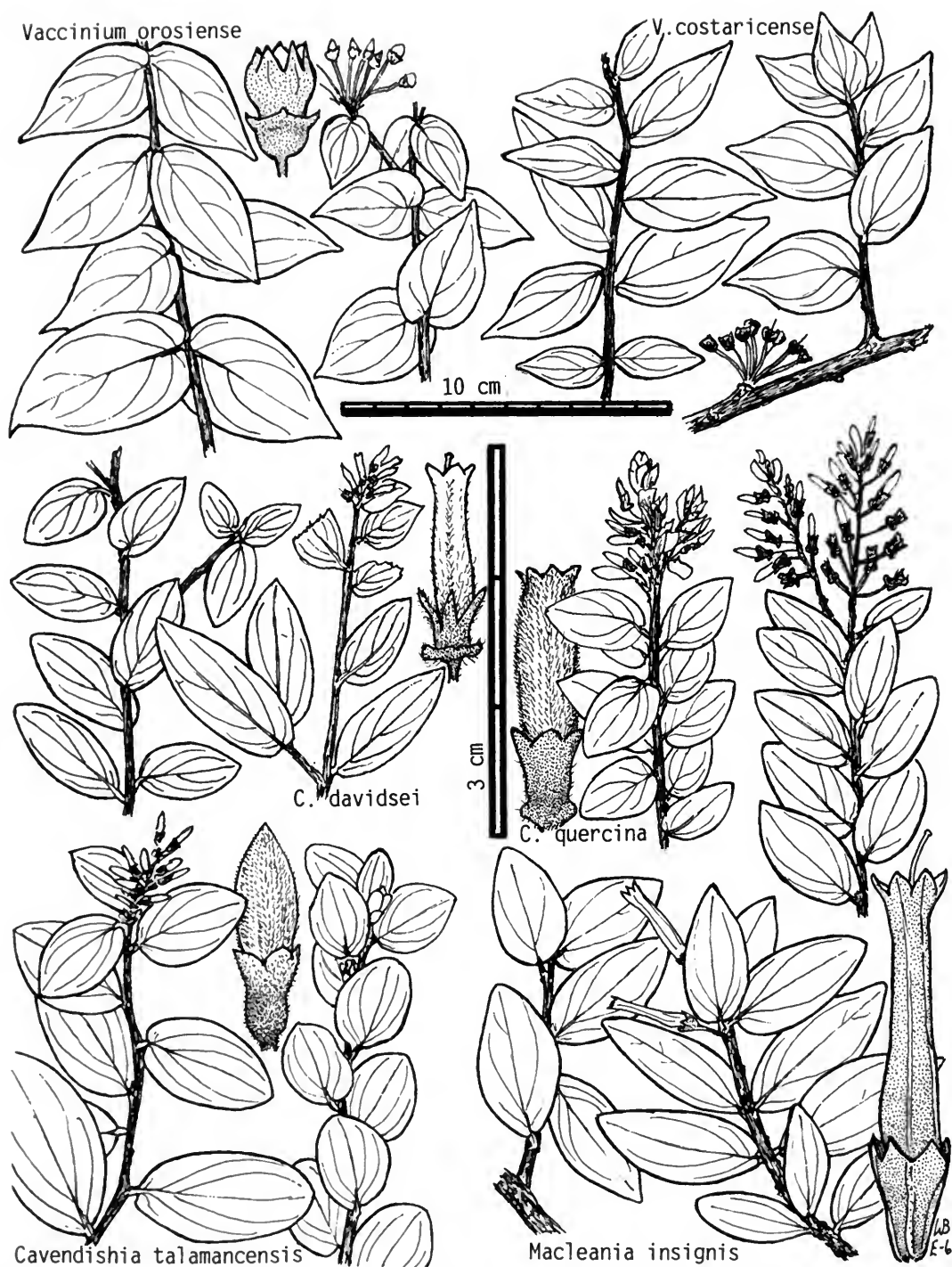


FIG. 6. Ericaceae shrubs with small to medium-sized leaves that are often rounded at the base: species of *Cavendishia*, *Macleania*, and *Vaccinium*.



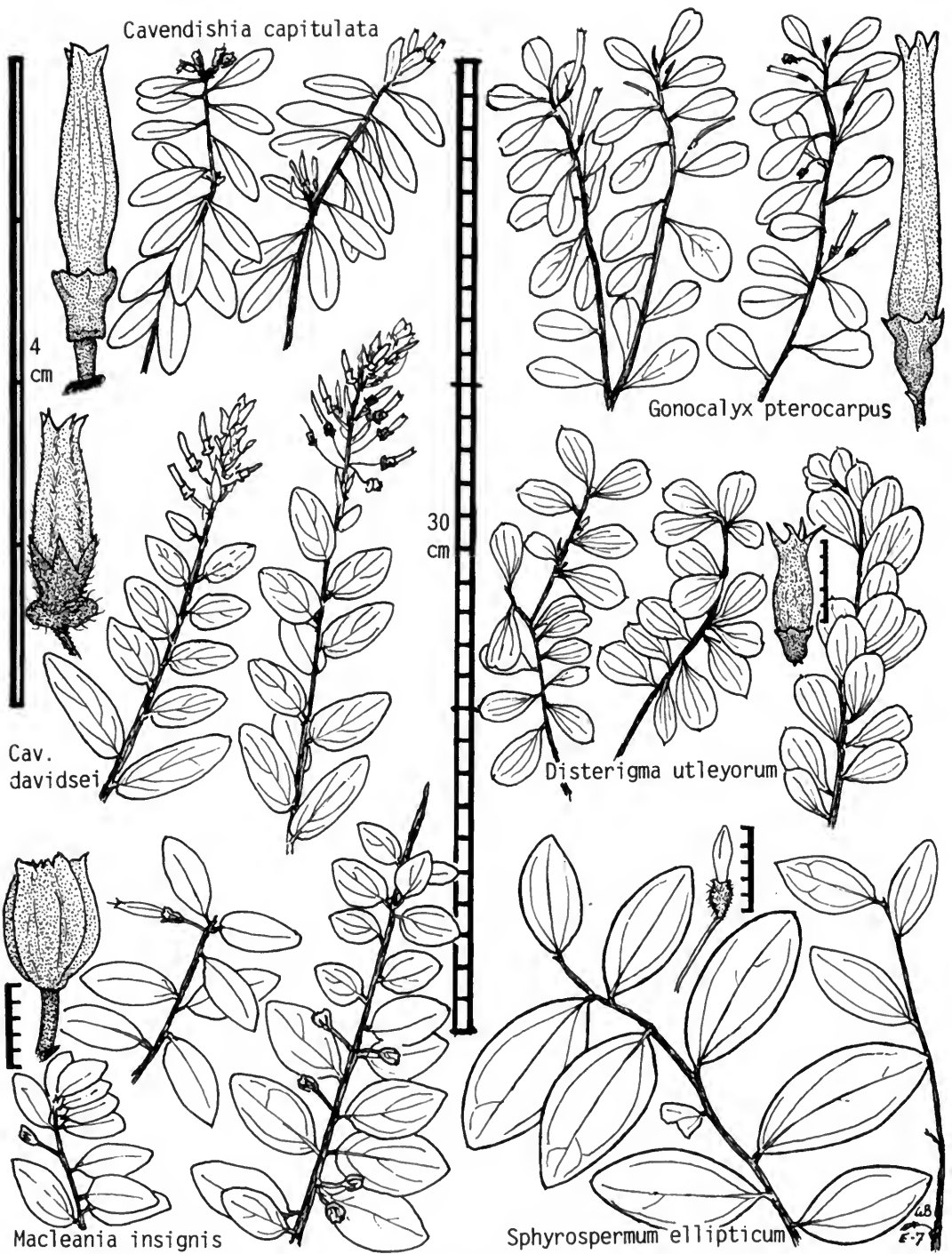


FIG. 7. Ericaceae shrubs with small to medium-sized leaves and with rounded or obtuse apicels: species of *Cavendishia*, *Disterigma*, *Gonocalyx*, *Macleania*, and *Sphirospermum*.

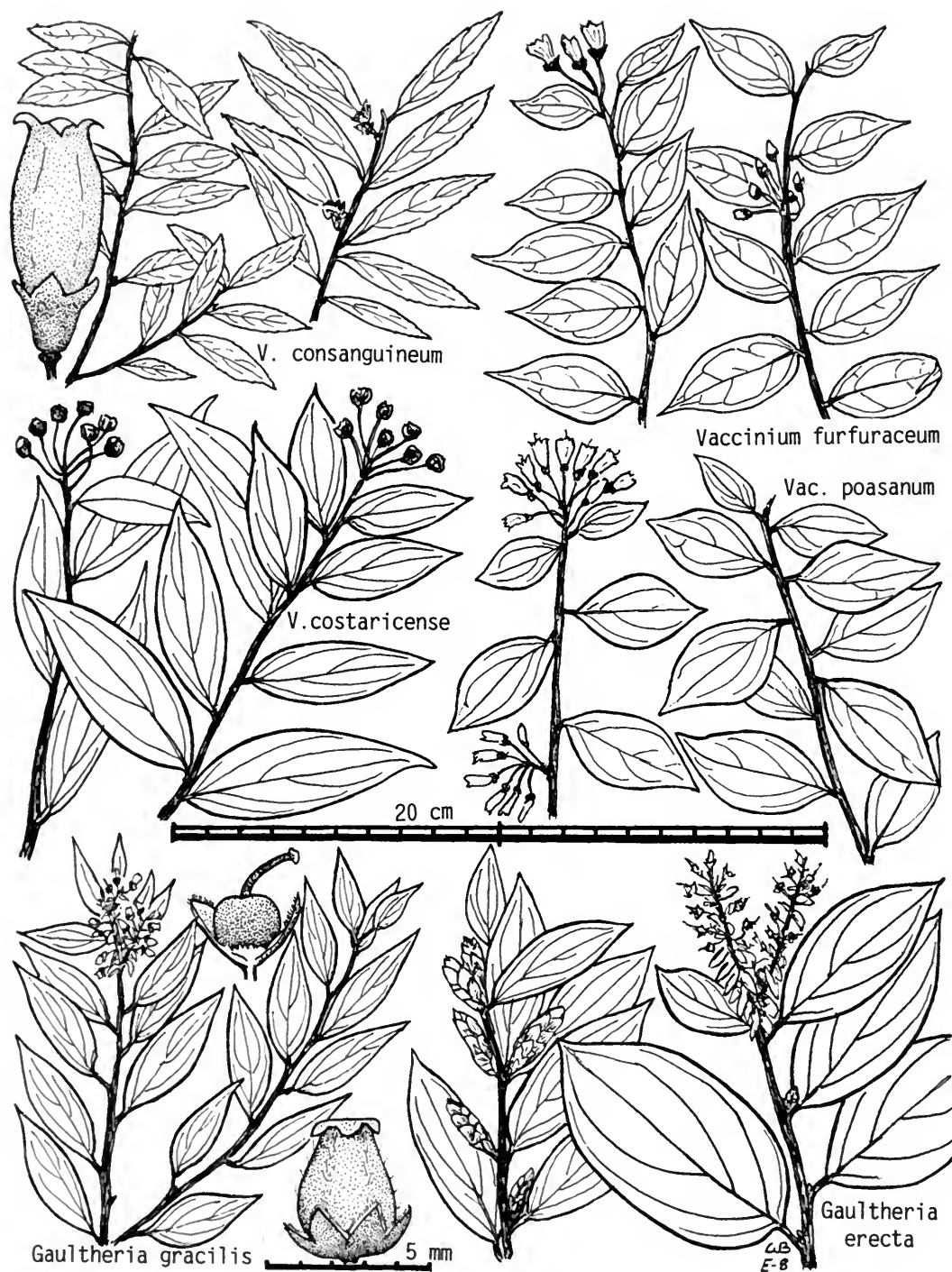


FIG. 8. Ericaceae shrubs with smaller to medium-sized leaves and acute or acuminate apices: species of *Gaultheria* and *Vaccinium*.

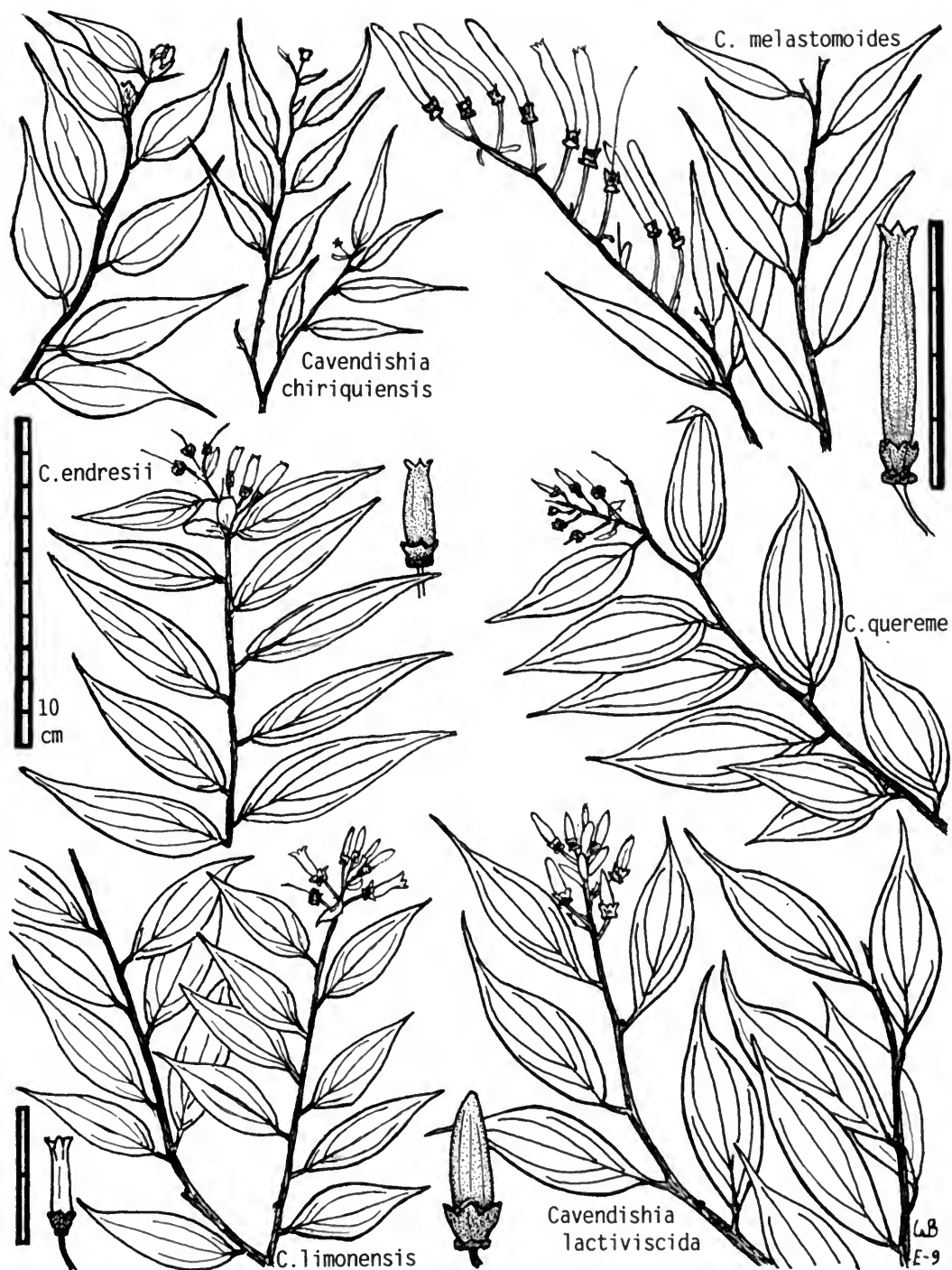


FIG. 9. Species of *Cavendishia* with medium-sized leaves with long-acuminate apices.

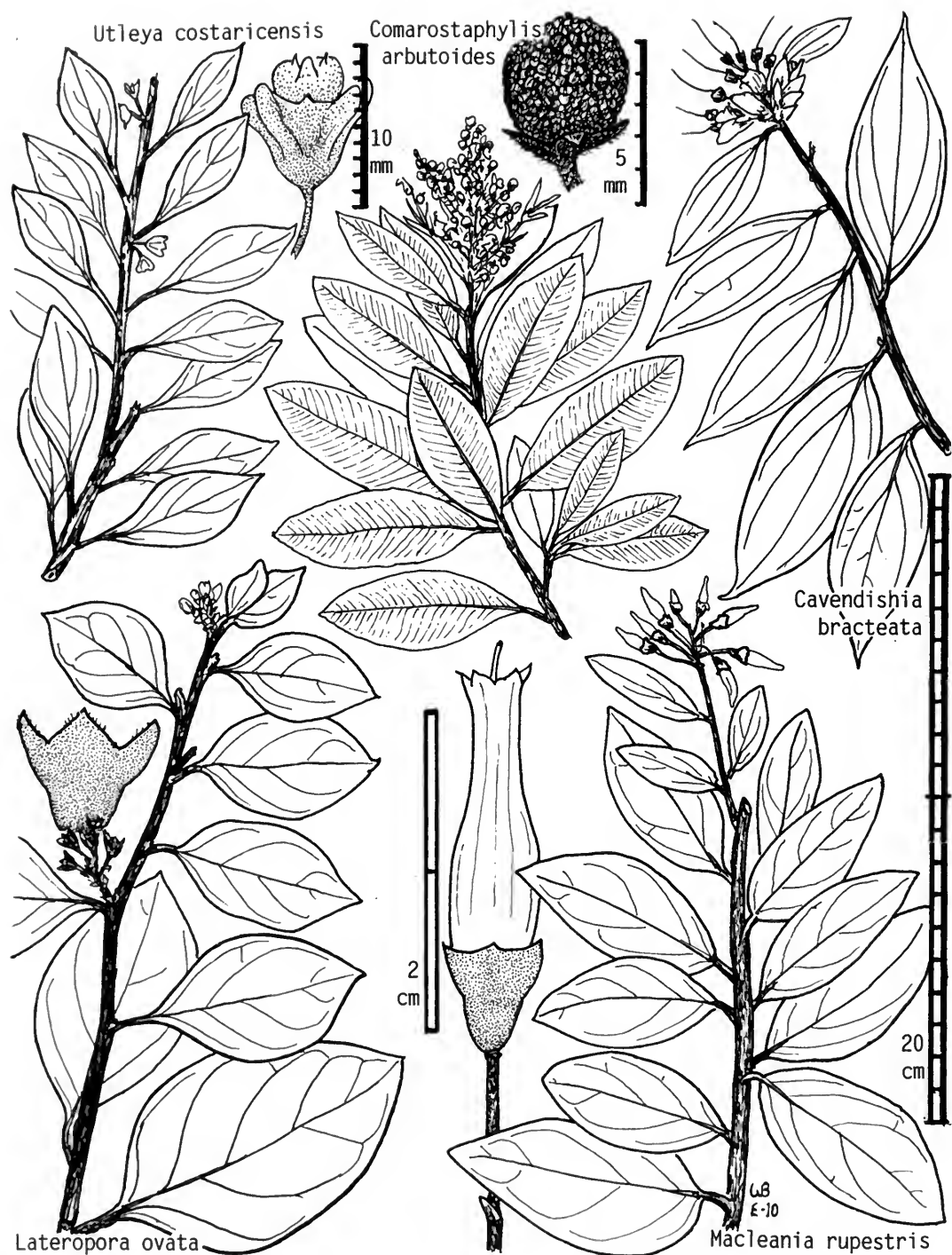


FIG. 10. Ericaceae shrubs with medium-sized leaves and with prominent petioles: species of *Cavendishia*, *Comarostaphylis*, *Lateropora*, *Macleania*, and *Utleya*.

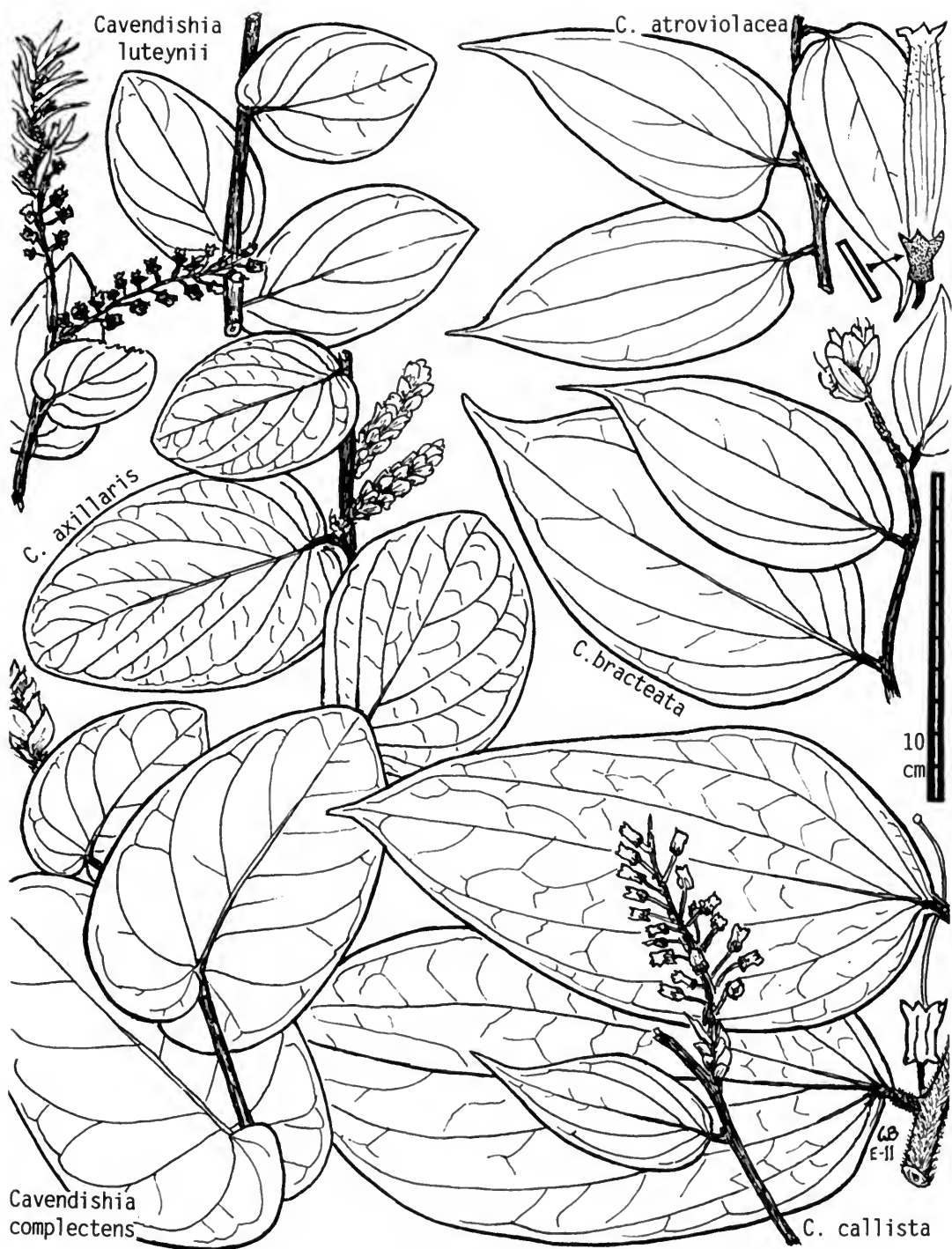


FIG. 11. Species of *Cavendishia* with medium or larger leaves with rounded or obtuse bases.



FIG. 12. Ericaceae shrubs with larger lanceolate leaves: species of *Cavendishia* and *Thibaudia*.

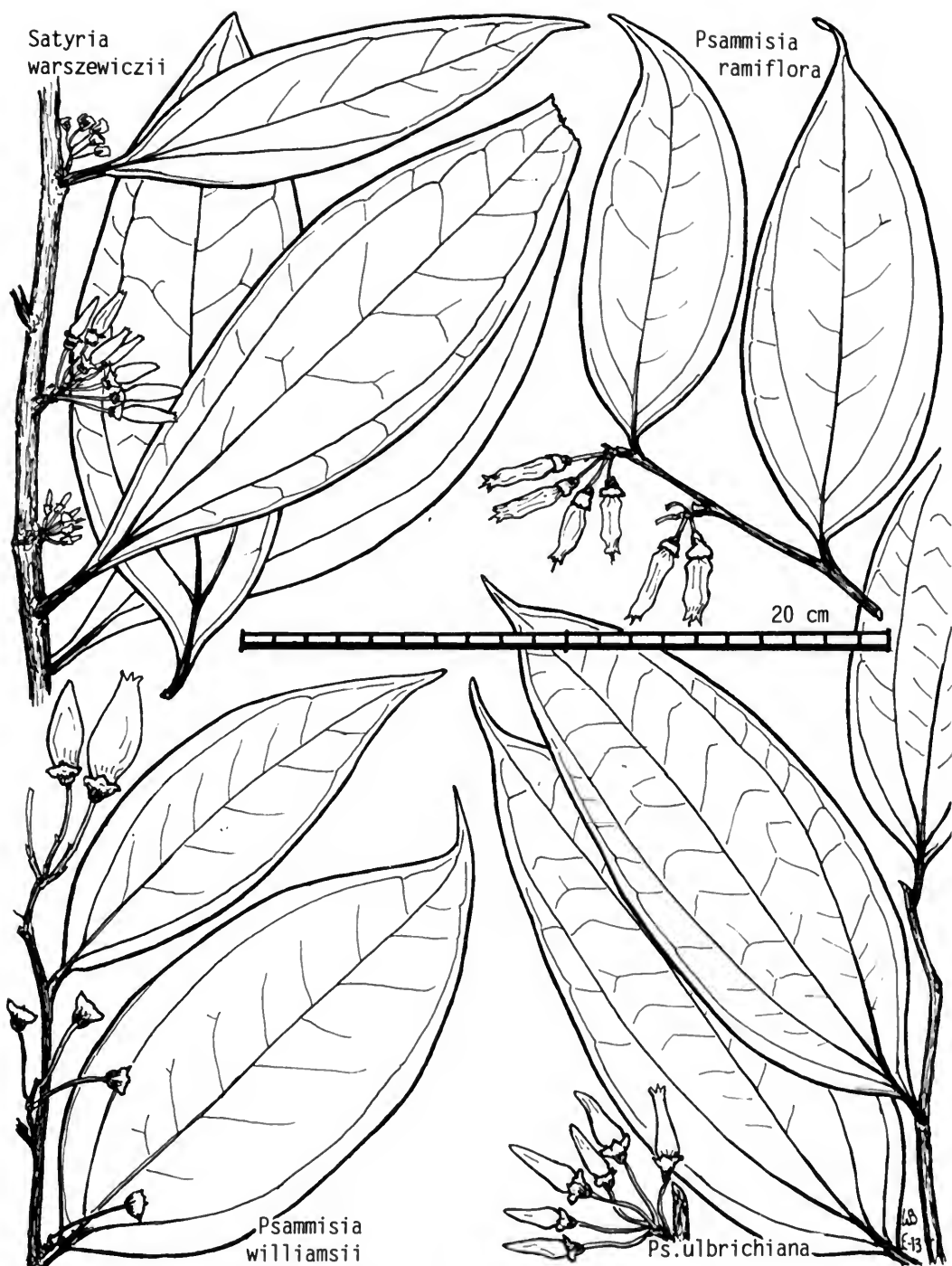


FIG. 13. Ericaceae shrubs with larger narrowly ovate or elliptic leaves: species of *Psammisia* and *Satyria*.



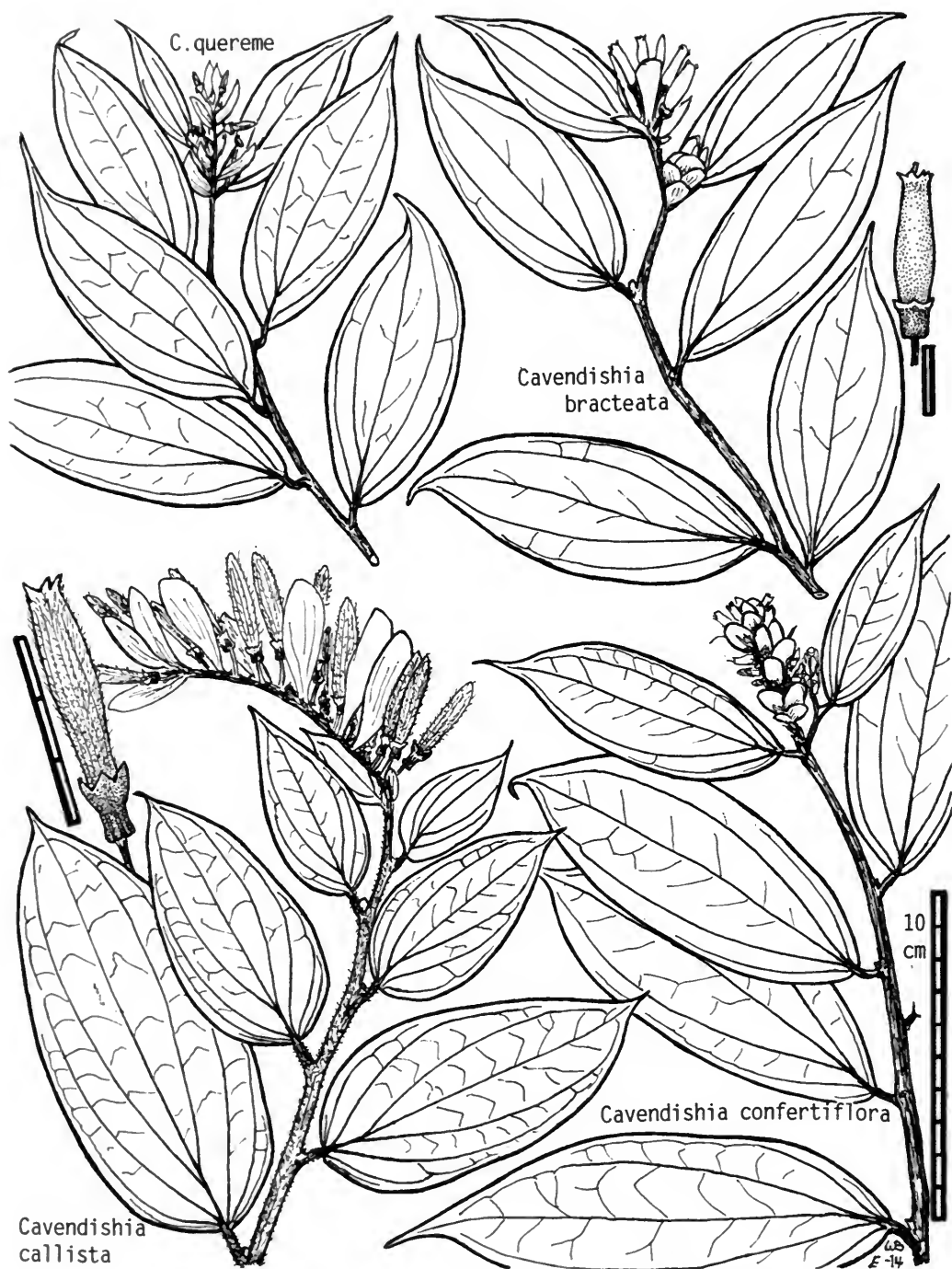


FIG. 14. Species of *Cavendishia* with larger leaves with acuminate apices.





FIG. 15. Two species of *Satyria* and some unusual Ericaceae of *Anthopterus*, *Cavendishia*, *Chimaphila*, and *Monotropa*.

are usually hidden among the mosses within which it grows, whether terrestrially or on mature tree branches.

Hybridization is not, in general, common in Costa Rican ericads but does occur sporadically in highly disturbed habitats where sympatry occurs. It has been recognized mostly in the genus *Cavendishia* (Luteyn, 1976c, 1983), based on field observations of plants with intermediate morphologies and then later confirmed by measurements of intermediate characters and of pollen viability in the laboratory. Hybrids are discussed with their parental species.

[Note: Descriptions are in general comparable; however, when one or two species in a genus have striking features not found in the other species, these are mentioned only where they occur, and it can be assumed that other species in the genus do not have this feature. All measurements were taken from dried herbarium material unless other-

wise stated by "when fresh," which means material preserved in alcohol. In this family, there is only a small degree of shrinkage once material dries. Overall calyx length is measured from the base of the calyx tube to the tip of the calyx lobes (i.e., the measurement includes both the calyx tube and limb). In similar fashion, overall corolla length is measured from the base of the corolla to the tip of the corolla lobes; corolla width is measured at the widest point. For corollas, the terms unistratose and bistratose are used when one or two layers or strata (respectively) are observable in the tissue; a longitudinal section of the corolla will show this to the naked eye, but it is easily seen without sectioning in the area between the corolla lobes where a bistratose corolla has tissue between the lobes like webbing between the toes of a duck. Overall stamen length is measured from the base of the filament to the tip of the anther. Overall anther length includes the theca plus tubule lengths.]

Key to Genera of Ericaceae in Costa Rica

- 1a. Plants lacking chlorophyll (whitish, pinkish or reddish, or at least not green), succulent herbs, mycotrophic ..... *Monotropa uniflora*
- 1b. Plants with chlorophyll (green), woody subshrubs, shrubs to trees, autotrophic ..... 2
- 2a. Plants subshrubs, with  $\pm$  herbaceous habit ..... *Chimaphila maculata*
- 2b. Plants shrubs or rarely trees, with woody habit ..... 3
- 3a. Ovary superior; fruit usually with perianth scars at base ..... 4
- 3b. Ovary inferior; fruit usually with perianth scars at apex ..... 8
- 4a. Petals free, usually 7-merous, usually wide-spreading; fruit a depressed obovoid or depressed globose, septicidally 5-7-valvate capsule ..... *Bejaria aestuans*
- 4b. Petals united, usually 4-5-merous; fruit a cylindrical septicidal or loculicidal capsule, drupe, or berry ..... 5
- 5a. Corolla salverform, slightly bilaterally symmetrical; fruit a cylindrical, septicidal capsule; viscin threads mixed with pollen tetrads [infrequently cultivated in Costa Rica and not included in the text] ..... *Rhododendron simsii*
- 5b. Corolla urceolate, cylindric-urceolate, or tubular, radially symmetrical; fruit a loculicidal capsule, drupe, or berry; viscin threads absent ..... 6
- 6a. Inflorescences terminal panicles; surface of ovary and fruit papillate; fruit a drupe; leaf blade usually >3 times longer than wide, usually >10 times longer than the petiole ..... *Comarostaphylis arbutoides*
- 6b. Inflorescences axillary racemes or flowers solitary; surface of ovary and fruit smooth; fruit a berry or capsule; leaf blade usually <3 times longer than wide, usually <10 times longer than the petiole ..... 7
- 7a. Fruit a berry, rarely with calyx becoming fleshy at base, but never surrounding the berry ..... *Pernettya prostrata*
- 7b. Fruit a capsule, surrounded by the fleshy calyx ..... *Gaultheria*
- 8a. Stamens strongly unequal, with filaments and/or anthers conspicuously alternately unequal ... 9
- 8b. Stamens equal, with filaments and anthers of equal lengths (rarely anthers inconspicuously alternately unequal) ..... 11

- 9a. Filaments and anthers unequal; stamens as long as corolla or rarely  $\frac{1}{2}$ – $\frac{1}{3}$  the corolla length; floral bracts usually large, showy ..... *Cavendishia*
- 9b. Filaments equal or unequal; anthers unequal or essentially equal; stamens usually about  $\frac{1}{3}$  as long as corolla; floral bracts small, inconspicuous ..... 10
- 10a. Calyx limb 5-parted; staminal filaments equal and connate over entire length; anthers unequal, with tubules widening apically but otherwise hardly distinguishable from thecae; floral bracts usually persistent; inflorescences often ramiflorous ..... *Satyria*
- 10b. Calyx limb 3-parted (in ours); staminal filaments unequal and distinct; anthers essentially equal, with tubules with parallel sides and easily distinguishable from thecae; floral bracts usually deciduous; inflorescences from the axils of leaves ..... *Orthaea*
- 11a. Anthers dehiscent by longitudinal slits that extend the entire length of the thecae; tubules rudimentary, apparently nonfunctional, <0.8 mm long ..... *Lateropora*
- 11b. Anthers dehiscent by pores or slits on the tubules and not extending onto thecae; tubules conspicuous, well-developed, >1 mm long ..... 12
- 12a. Anthers dehiscent by latrorse clefts that do not extend to tip of tubule ..... *Didonica*
- 12b. Anthers dehiscent by terminal pores or introrse clefts (or if clefts latrorse, then extending to tip of tubule) ..... 13
- 13a. Bracteoles located at apex of pedicel, clasping and surrounding calyx (and sometimes lower corolla) ..... *Disterigma*
- 13b. Bracteoles located well below apex of pedicel, or if apical then not clasping calyx ..... 14
- 14a. Tubules elongate, thin, about half as wide (or less) as thecae ..... *Gonocalyx*
- 14b. Tubules about as wide as thecae, or if narrower then much shorter than thecae ..... 15
- 15a. Thecae conspicuously papillate; tubules rigid, elongate- to short-conical, distinct or sometimes laterally connate or fused into one tubule; stamens often  $\frac{1}{3}$ – $\frac{1}{2}$  as long as corolla ..... 16
- 15b. Thecae smooth to minutely papillate; tubules flexible, cylindric, elongate to short, distinct to base or fused into one tubule in *Themistoclesia pentandra*; stamens usually as long as corolla ... 17
- 16a. Connectives never spurred; tubules usually laterally connate (the septum visible) or sometimes totally fused into one; corolla cylindric or angled, gradually narrowed to apex ..... *Macleania*
- 16b. Connectives alternately spurred, rarely all spurred, if spurs absent then connectives usually apically prolonged or thickened; tubules distinct to base; corolla cylindric, never angled and often abruptly constricted to apex, or corolla  $\pm$  globose to conical (and then <1 cm long) ..... *Psammisia*
- 17a. Calyx continuous with pedicel (pedicel not jointed at apex) ..... 18
- 17b. Calyx articulate with pedicel (pedicel jointed at apex) ..... 20
- 18a. Calyx terete; pedicels proportionally long, thin, filiform and pendent, rarely short and 1–4 (8) mm long, but then corolla dark red and campanulate ..... *Sphyraspermum*
- 18b. Calyx angled or winged; pedicels short or long, but thick, not filiform and pendent (rarely 9–22 mm long) ..... 19
- 19a. Leaves (0.7) 1–4.5 cm long, usually distichous (spiral in *T. pentandra*) along stem, base of lamina without glands; calyx usually angled (winged in *T. pentandra*), 3.2–7 mm long; corolla terete to pentagonal, the lobes ca.  $\frac{1}{10}$ – $\frac{1}{3}$  overall corolla length, not strongly reflexed as to expose stamens at anthesis ..... *Themistoclesia*
- 19b. Leaves 5–13 cm long, spirally arranged along stem, base of lamina beneath with 1 or 2 pairs of circular, concave glands; calyx 5-winged, 5–7 mm long; corolla broadly to narrowly 5-winged, the lobes ca.  $\frac{1}{3}$  overall corolla length, strongly reflexed thus exposing stamens at anthesis ..... *Anthopterus*
- 20a. Corolla ca. 4 mm long, the tube conspicuously spurred apically opposite the lobes; calyx conspicuously winged ..... *Utleia costaricensis*
- 20b. Corolla >7 mm long, never spurred; calyx usually terete ..... 21
- 21a. Corolla urceolate to cylindric-campanulate, the lobes imbricate or valvate; staminal filaments usually distinct ..... *Vaccinium*
- 21b. Corolla elongate-tubular, the lobes valvate; staminal filaments connate ..... *Thibaudia costaricensis*

# Anthopterus Hook

REFERENCES—J. L. Luteyn, New species and notes on neotropical Ericaceae. *Opera Bot.* 92: 109–113. 1987 [*Anthopterus*, pp. 109–113]. J. L. Luteyn, New species, new records, and neotypification of some Mesoamerican Ericaceae. *Brittonia* 48: 241–249. 1996 [*Anthopterus*, p. 248]. J. L. Luteyn, Redefinition of the neotropical genus *Anthopterus* (Ericaceae: Vaccinieae), including one new species. *Brittonia* 48: 605–610. 1996 [1997].

Terrestrial or epiphytic **shrubs**. **Leaves** alternate (in ours), subopposite, or verticillate, petiolate, the blade with entire margin, the venation plinerved or pinnate, the base beneath with 1 or 2 pairs of circular, concave glands. **Inflorescences** axillary, racemose, many-flowered; floral bract small and inconspicuous; pedicels continuous with calyx; bracteoles 2, medial to submedial (in ours). **Flowers** 5-merous, without odor; calyx tube broadening apically, 5-winged opposite the sinuses, limb suberect, lobes ovate to deltate; **corolla** sympetalous, aestivation valvate, subcylindric, cylindric-urceolate or subglobose, broadly 5-winged opposite the lobes, lobes ca.  $\frac{1}{2}$  overall corolla length, strongly reflexed thus exposing stamens at anthesis; **stamens** 10, essentially equal, nearly as long as the corolla, sometimes geniculate; filaments equal, distinct or slightly connate at base, shorter than anthers; connectives lacking disintegration tissue or spurs; anthers dorsifixed, membranous, lacking awns, thecae smooth, tubules 2, distinct, about as wide as and usually longer than thecae, dehiscing by introrse,

elongate clefts; pollen grains in tetrahedral tetrads, lacking viscin threads; ovary inferior; style filiform, about as long as the corolla; stigma truncate; nectariferous disc annular or cupuliform. **Fruit** a berry, usually purplish; seeds numerous, small.

*Anthopterus* is a genus of 12 species ranging from northeastern Costa Rica to north-central eastern Peru. It is characterized by having the pedicel continuous with the calyx, and a winged calyx tube and corolla. *Anthopterus costaricensis* and *A. revolutus* are the first records of this genus in Costa Rica. Both species belong to subgen. *Anthopterus*, which is characterized by having alternate leaves, 1 or 2 pairs of circular, concave glands at the base of the lamina, a corolla that is pale yellowish-green throughout and with wings broadest basally and narrowing apically, the lobes strongly reflexed thus exposing the stamens at anthesis, and straight stamens. Subgenus *Gonandra* Luteyn occurs from extreme southeastern Panama (Darién Prov.) to north-central Ecuador (Luteyn, 1996c). Because of the paucity of collections of any of the species, the range of variation within the genus is unknown. *Anthopterus* is morphologically similar to *Thibaudia* and *Themistoclesia*, but it is separated from them by its combination of nonarticulate (i.e., continuous) calyx, conspicuously 5-winged calyx tube, and 5-winged corolla.

## Key to the Species of *Anthopterus*

- 1a. Leaf blades narrowly elliptic to oblanceolate, strongly revolute, to 1.5 cm wide, not amplexicaul; petioles 3–4 mm long ..... *A. revolutus*
- 1b. Leaf blades elliptic to oblong-elliptic, flat, 3–4.5 cm wide, clasping and amplexicaul; petioles to 2 mm long ..... *A. costaricensis*

***Anthopterus costaricensis*** Luteyn, *Brittonia* 48: 609. 1996[1997].

Epiphytic **shrubs**; mature stems subterete, bluntly and broadly ribbed, glabrous; twigs subterete, complanate, bluntly angled, striate, glabrous, with scattered ovate-lanceolate, long-acuminate perulae to 10 mm long proximal to first leaves. **Leaves** with petioles subterete, strongly flattened adaxially, rugose, to 2 mm long, glabrous; leaf blades coriaceous, subsessile, clasping or amplexicaul, flat, elliptic to oblong-elliptic, (7) 9–12 cm long, 3–4.5 cm wide, base rounded, cordate, auriculate, apex obtuse or bluntly acute, glabrous but densely and deciduously glandular-fimbriate on both surfaces, weakly 5 (7)-plinerved (or pinnately nerved with 2–3 secondary nerves per side), midrib impressed above and

conspicuously raised beneath, lateral nerves and reticulate veinlets slightly raised on both surfaces. **Inflorescence** solitary, 12–21-flowered; rachis subterete, angled, striate, bracteate, overall 4.5–11 cm long but the basal 3.5 cm usually naked and lacking fertile nodes, glandular-fimbriate throughout; floral bract apparently persistent, narrowly ovate, 3–5 mm long, apex long-acuminate, glabrous, margin weakly glandular-fimbriate; pedicels subterete, angled, striate, 16–22 mm long (post anthesis), glandular-fimbriate; bracteoles near middle, similar to floral bract but 2.5–3 mm long. **Flowers** (all post anthesis) with calyx ca. 7 mm long, glabrous, glandular-fimbriate, tube obconical, strongly 5-winged, ca. 5 mm long, limb erect, ca. 2 mm long, lobes ovate, apiculate, ca. 1.5 mm long, sinuses acute; **corolla**, stamens, and berry not seen.

*Anthopterus costaricensis* is found in premon-

tane forest, 1200 m elevation. It is endemic to Costa Rica and is known from only the type collection: Limón Province: Cantón Talamanca, between Cerro Chimú and Cerro Matama, *L. D. Gómez & Herrera 23557* (NY). The type was collected in late flower in late April. **Endangered.**

*Anthopteris costaricensis* is characterized by its clasping to amplexicaul, elliptic to oblong-elliptic, flat (not revolute) leaves, and twigs with scattered, long-acuminate perulae (to 10 mm long) proximal to the first leaves. It is morphologically most similar to *A. pterotus* (A. C. Smith) Luteyn from Colombia, a species also with sub-amplexicaul leaves but with a peculiar paniculate type of inflorescence. Although neither corollas nor stamens are known from *A. costaricensis*, the general morphology of the plant and especially the distinctive calyx tube place it in *Anthopteris* subgen. *Anthopteris* following Luteyn (1996c).

***Anthopteris revolutus*** (Wilbur & Luteyn) Luteyn, Fl. Ecuador 54: 387. 1996. *Themistoclesia revoluta* Wilbur & Luteyn, Ann. Missouri Bot. Gard. 68: 164. 1981. Figures 2Q and 15.

Epiphytic **shrubs**; mature stems subterete, coarsely ridged and grooved but becoming terete, glabrous, minutely puberulent, or short-pubescent; twigs subterete, bluntly and coarsely angled, puberulent; axillary buds supraxillary, the scales lanceolate, acuminate, ca. 3 mm long. **Leaves** with petioles flattened adaxially and canaliculate, 3–4 mm long, glabrous to inconspicuously puberulous to short-pubescent; leaf blades coriaceous, narrowly elliptic to oblanceolate, strongly revolute so as to conceal actual margin, 5–13 cm long, 0.6–1.5 cm wide, base cuneate or rounded, apex obtuse to rounded, glabrous above or moderately to densely short-pubescent on both surfaces, glabrate, sparingly to moderately beset with reddish-brown, appressed, glandular fimbriae, 0.1–0.2 mm long, pinnately nerved, midrib prominently impressed above and raised beneath, secondary nerves and reticulate veinlets raised to impressed above and moderately so but obscure beneath. **Inflorescences** 10–16-flowered, surrounded by 6–8, appressed, lanceolate to narrowly triangular, acute, 3.5–5 mm long, finely short-pubescent bracts; rachis ridged or striate, 5–10 cm long, moderately to densely short-pubescent with white to hyaline trichomes 0.2–0.5 mm long, also with scattered glandular fimbriae; floral bract narrowly triangular to narrowly lanceolate, 2.5–4 mm long, apex long-acuminate, glabrous to short-pilose above, ciliate; pedicels 9–16 mm long, moderately to densely spreading short-pubescent with white to hyaline trichomes 0.2–0.3 mm long, also with scattered glandular fimbriae; bracteoles medial to submedial, appressed, narrowly triangular, 2–3 mm long, apex acute to acuminate, spreading short-pubescent. **Flowers** with calyx 5–6 mm long, moderately spreading short-pilose throughout, also with scattered glandular fimbriae, tube obpyramidal to narrowly turbinate, strongly 5-angulate or winged, 4–5 mm long, limb

1–2 mm long, lobes narrowly triangular, acute to acuminate, sometimes apiculate, 1–2 mm long; **corolla** cylindric-urceolate, narrowly 5-winged (wings broadest at base), 7–9 mm long, ca. 4–4.5 mm diam. near base including wings, pale cream-green, glabrous, lobes 2.5–3 mm long, sparingly ciliate along midrib, strongly reflexed at anthesis exposing stamens and style; **stamens** 6–8.2 mm long, alternately slightly unequal; filaments equal, 1–2 mm long, sparsely ciliate and glandular-fimbriate; anthers 7.5–9 mm long, thecae 2.5–3 mm long, tapering into a short-setose, apiculate base, closely coherent at base due to interlocking of antheridial grooves, tubules 5–6 mm long, dehiscing by a narrow cleft ca. 1.5 mm long. **Berry** spherical, ca. 10 mm diam.

*Anthopteris revolutus* is found in primary moist forest to premontane forest, 900–1400 m elevation. It is distributed in Costa Rica, Panama, and Ecuador. In Costa Rica it is known from only one collection in Limón Province (road from Fila Dimat toward Soki via Quebrada Sha, *L. D. Gómez et al. 23871*). Flowering specimens have been collected in February, March, and August (in Panama). **Endangered.**

*Anthopteris revolutus* is characterized by having narrow, strongly revolute leaf blades with pinnate venation and basally cuneate bases, long-pedicellate flowers borne in elongate racemes, and glandular-fimbriate staminal filaments. It is most closely related to *A. schultzeae* (Sleumer) Luteyn from eastern Ecuador and adjacent Peru.

## **Bejaria Mutis ex Linnaeus** nom. & orth. conserv.

REFERENCES—R. Mansfeld & H. O. Sleumer, Revision der Gattung *Befaria* Mutis. Notizbl. Bot. Gart. Berlin-Dahlem 12: 235–276. 1935. S. E. Clemants, (1103) Proposal to conserve 6182 *Bejaria* (Ericaceae) with a conserved spelling and type. Taxon 43: 473–476. 1994. S. E. Clemants, *Bejaria*. Fl. Neotrop. Monogr. 66: 54–106. 1995.

Terrestrial **shrubs** or small, slender **trees**, glabrous to densely glandular-setose. **Leaves** alternate, petiolate, the blade flat to tightly revolute, margin entire or rarely obscurely denticulate, the venation pinnate. **Inflorescences** terminal or axillary (in ours), racemose to corymbose (in ours) or rarely paniculate, few- to many-flowered, often viscid; floral bract small and inconspicuous; pedicels continuous with calyx; bracteoles 2. **Flowers** (5) 7 (8)-merous, mildly fragrant only in some populations of *B. aestuans*; calyx synsepalous, persistent in fruit, deeply lobed, the lobes much longer than tube, separate or imbricate at anthesis; **corolla** polypetalous, aestivation imbricate, the petals showy, these suberect and imbricate (hummingbird pollinated) or (in ours) spreading (bee

pollinated) at anthesis, soon deciduous; **stamens** twice as many as petals or more (10–20), equal, about as long as petals or longer; filaments equal, distinct, elongate, basally densely pilose or tomentose; connectives lacking disintegration tissue or spurs; anthers dorsifixed, equal, oblong-obconic, dehiscent somewhat introrsely by slightly oblique, somewhat teardrop-shaped, terminal pores, interior rim of pores whitish; pollen grains in tetrahedral tetrads, with viscin threads; ovary superior, 6–7-locular, with axile placentation, glabrate; style elongate and often bent to one side, glabrous; stigma capitate, 6–7-grooved; nectariferous disc surrounding ovary base, unlobed. **Fruit** a capsule, depressed obovoid or depressed globose, woody, septicidally 5–7-valvate from apex; seeds numerous, winged or tailed.

*Bejaria* (formerly called *Befaria*) is a neotropical to subtropical genus of 15 species, ranging from Georgia and Florida (U.S.A.) to Cuba, from Mexico south into Bolivia, and east to Guyana. The genus has not yet been found in Costa Rica, although one species does occur in western Chiriquí Province, Panama. *Bejaria* is characterized by having a usually 7-merous corolla with free petals, nonappendaged anthers, viscin threads mixed with pollen tetrads, superior ovary, and septicidally dehiscent, capsular fruits. Within the Ericaceae, *Bejaria* is placed in subfamily Ericoideae, where it resides as an isolated genus in the tribe Bejarieae (Kron et al., 2002a).

***Bejaria aestuans*** Linnaeus, Mont. Pl. 242. 1771. *Bejaria glauca* Bonpland in Humboldt & Bonpland, Pl. Aequinoct. 2: 118, pl. 117. 1813 (as *Befaria*). Illustrated: R. L. Wilbur & J. L. Luteyn, Ann. Missouri Bot. Gard. 65: 39, fig. 4. 1978. S. E. Clemants, Fl. Neotrop. Monogr. 66: 75, fig. 7. 1995. Figures 1C and 4.

**Shrub** to small **tree** 5–6 m tall; mature stems glabrous, tomentose, or hispid to glandular-hispid; twigs terete, coarsely ribbed, densely ferrugineous-tomentose, glabrate, sometimes glandular-hispid. **Leaves** with petioles subterete, slightly winged, 5–10 mm long, ferrugineous-tomentose when immature, glabrate; leaf blades coriaceous, flat or sometimes slightly revolute, elliptic to lanceolate or oblanceolate, lance-elliptic or rarely ovate, 2–5 cm long, 0.8–1.5 cm wide, base long-cuneate and decurrent, apex acute to short-acuminate, often bluntly short-mucronate, both surfaces glabrous to tomentose, hispid, or glandular-hispid when young, then often glabrate, often glaucous beneath, midrib impressed above and conspicuously raised beneath, reticulate veinlets obscure on both surfaces. **Inflorescences** short-racemose or subcorymbose, 10–20-flowered; rachis subterete, coarsely angled, 1.5–2.5 cm long, densely ferrugineous-tomentose to glabrate; floral bract elliptic to lanceolate or oblanceolate, 2–5 mm long, ca. 1 mm wide, sometimes leaf-like and up to 30 mm long and 8.4 mm wide, apex acute to obtuse, sometimes acuminate, ciliate to

glandular-ciliate, ferrugineous-tomentose on both surfaces; pedicels subterete, striate, 15–24 mm long, ca. 0.5 mm diam., glabrous, densely ferrugineous-tomentose, hispid, or glandular-hispid, glabrate; bracteoles at or below middle, elliptic to oblanceolate, 2–5 mm long, ca. 1 mm wide, apex acute to obtuse, sometimes acuminate, ciliate to glandular-ciliate, ferrugineous-tomentose on both surfaces. **Flowers** erect, 7-merous; calyx 2–3 mm long, glabrous, densely ferrugineous-tomentose, hispid, glandular-hispid, glabrescent, the lobes ovate, 1.5–2 mm long, apex obtuse, margin ciliate; **corolla** spreading-campanulate, the petals obovate, 15–20 mm long, 5–6 mm wide, densely ciliate at apex, white to dark rose-pink; **stamens** subequal to corolla or slightly exserted, 15–21 mm long; filaments 13–20 mm long, densely pilose in the basal third; anthers ca. 2 mm long; style subequal to corolla or exserted, 21–22 mm long, glabrous. **Capsule** depressed-obloid, 7–8 mm diam.

*Bejaria aestuans* is found in pine woods, cloud forest, dry montane forest, shrub páramo, grasslands, and disturbed roadsides, (300) 1000–3000 (3500) m elevation (Continental Divide cloud forest at 1200–1700 m in Panama). It is geographically the most widespread and morphologically the most variable species in the genus, ranging from west-central Mexico almost continuously to Bolivia. It is very rare in El Salvador, Nicaragua, and Panama and has yet to be collected in Costa Rica. In western Panama, flowering specimens have been collected in January, May, July, and August; fruiting in January, July, and August. **Endangered** (in Panama).

Mansfeld and Sleumer (1935) recognized five varieties within the species that were distinguished primarily by characters of indumentum. This character is unusable as its facies change with the age of the plant. Therefore, the varieties of *B. aestuans* were not recognized by Clemants (1995) in his revision of the genus. The description above is based on Panamanian collections. In Panama, *B. aestuans* is characterized by having obscure floral bracts, petals that are fully separate and light to dark pink in color, stamens about equaling the corolla in length, and eglandular, ferrugineous-tomentose pubescence that varies from dense on young parts to glabrate on older parts. The flowers have a sweet odor and are visited by bees (pers. observ.).

## ***Cavendishia* Lindley** nom. conserv.

REFERENCES—J. L. Luteyn, The genus *Cavendishia* (Vacciniaceae) in Costa Rica. Brenesia 6:

9–18. 1975. J. L. Luteyn, Ericaceae—Part I. *Cavendishia*. Fl. Neotrop. Monogr. 35: 1–290. 1983. J. L. Luteyn, New species, new records, and neotypification of some Mesoamerican Ericaceae. Brittonia 48: 241–249. 1996. J. L. Luteyn & J. F. Morales, Four new species of *Cavendishia* (Ericaceae: Vaccinieae) from Costa Rica. Brittonia 48: 514–519. 1996[1997].

Terrestrial or epiphytic **shrubs**. **Leaves** alternate, petiolate, the blade sometimes revolute, margin entire, the venation plinerved or pinnate. **Inflorescences** axillary, usually solitary, racemose or subfasciculate; floral bracts usually large and showy; pedicels articulate with calyx; bracteoles 2, basal or rarely medial. **Flowers** 5-merous, without odor; calyx with tube apophysate or not, lobes erect or connivent after anthesis, often glandular; **corolla** sympetalous, aestivation valvate, cylindric, usually car-nose when fresh; **stamens** 10, subequal or strongly unequal to each other, about equaling corolla in overall length or rarely  $\frac{1}{2}$ – $\frac{1}{3}$  corolla length; filaments usually distinct (rarely slightly coherent near base), alternately unequal; connectives lacking disintegration tissue or spurs; anthers alternately unequal, lacking awns, thecae smooth or minutely papillate, tubules 2, distinct, about same width as thecae and about twice as long, dehiscing introrsely by elongate clefts; pollen grains in tetrahedral

tetrads, lacking viscin threads; ovary inferior; style fili-form, usually as long as corolla, glabrous. **Fruit** a berry; seeds numerous, ca. 0.5–1.2 mm long.

*Cavendishia* includes about 130 species that range from Mexico to Bolivia, east to Guyana and Brazil. It is characterized by having alternately unequal staminal filaments and anthers and usu-ally conspicuously large floral bracts. The genus has been divided into several sections and series based mostly on characters of the calyx tube base (i.e., apophysate or nonapophysate) and the types of glands found especially on the calyx lobes (see Luteyn, 1983, for details and photos). In order better to understand these infrageneric relation-ships within *Cavendishia*, we present below a key to the sections and series found in Costa Rica and adjacent western Panama, as well as a second key to the species. *Cavendishia* is morphologically most similar to *Orthaea* Klotzsch and *Thibaudia* Ruiz & Pav. ex J. St.-Hil. The genus is the most commonly collected member of the Ericaceae in Costa Rica because of its abundance and showy nature. Twenty-two species are currently known in Costa Rica.

Key to the Sections and Series of *Cavendishia* in Costa Rica

- 1a. Calyx lobe margins eglandular or irregularly lacerate-glandular (then usually darker in color and thinner than the rest of the lobe), neither scarious, glandular-fimbriate, nor glandular-callose . . . . . sect. *Quereme*
- 1b. Calyx lobe margins scarious, glandular-fimbriate, or glandular-callose . . . . . 2
- 2a. Calyx lobe margins scarious or glandular-fimbriate, the fimbriae distinct (rarely caducous) or be-coming laterally fused and then sometimes forming a thin, supramarginal gland (sect. *Cavendishia*) . . . . . 3
- 2b. Calyx lobe margins glandular-callose **or** entire calyx lobe glandular-callose . . . . . 4
- 3a. Calyx lobes broadly overlapping at anthesis . . . . . ser. *Imbricatae*
- 3b. Calyx lobes not overlapping at anthesis . . . . . ser. *Cavendishiae*
- 4a. Calyx lobes completely glandular callose and this sometimes extending onto the calyx limb proper; plants without globular glands . . . . . sect. *Callista*
- 4b. Calyx lobes with callose glands along margins only, **or** the callose tissue sometimes extending onto the lobe lamina proper; if entire lobe glandular, then plants also bearing globular glands ca. 0.1–0.2 mm diam. (sect. *Engleriana*) . . . . . 5
- 5a. Sessile (or minutely peltate), subglobular glands 0.1–0.2 mm diam. along margins of floral bracts and bracteoles, rachises, pedicels, often also on the calyces, mature stems, and leaves (sometimes caducous from upper leaf surface but then leaving tiny, pustular scars, the exudate often milky-white) . . . . . ser. *Lactiviscidae*
- 5b. Globular glands not present as above . . . . . ser. *Englerianae*

## Key to the Species of *Cavendishia*

- 1a. Leaves amplexicaul, the bases strongly cordate ..... *C. complectens*
- 1b. Leaves subsessile to long petiolate, sometimes clasping to nearly amplexicaul, but never strongly amplexicaul and with bases strongly cordate ..... 2
- 2a. Margins of calyx lobes eglandular, glandular-fimbriate (fimbriae sometimes caducous), or lacerate-glandular ..... 3
- 2b. Margins, apex, or all of calyx lobes glandular callose-thickened, or with intermittent stout, oblong glandular thickenings ..... 14
- 3a. Calyx limb and floral bracts usually conspicuously striate; bracteoles striate, >5 mm long ..... *C. axillaris*
- 3b. Calyx limb and floral bracts smooth; bracteoles smooth, rarely >5 mm long ..... 4
- 4a. Leaf blade up to 6 (6.8) cm long, the apex obtuse, rounded, or broadly acute ..... 5
- 4b. Leaf blade usually longer than 6 cm, the apex sharply acute to long-acuminate ..... 9
- 5a. Base of calyx tube strongly apophysate; floral bracts 12–25 mm long ..... 6
- 5b. Base of calyx tube weakly or not apophysate; floral bracts 8–14 (19) mm long ..... 8
- 6a. Inflorescence pilose; rachis 3–9 cm long; pedicels 9–10 mm long; corolla 11–13 mm long ..... *C. davidsei*
- 6b. Inflorescence glabrous (calyx tube short-pilose in *C. gomezii*); rachis 0.3–2.5 cm long; pedicels 3–8 mm long; corolla 7.5–10 mm long ..... 7
- 7a. Leaves obviously petiolate, the blades neither clasping nor amplexicaul, flat; rachis 1–2.5 cm long; pedicels 6–8 mm long; calyx tube short-pilose; corolla 9–10 mm long ..... *C. gomezii*
- 7b. Leaves with petioles inconspicuous, the blades clasping to nearly amplexicaul, strongly bullate; rachis 3–6 mm long; pedicels 3–4.5 mm long; calyx tube glabrous; corolla 7.5–8 mm long ..... *C. luteynii*
- 8a. Rachis subfasciculate, <1 cm long, 3–6 (7)-flowered; floral bracts 11 mm or more long; leaves flat; calyx and corolla glabrous; calyx lobes densely glandular-fimbriate ..... *C. capitulata*
- 8b. Rachis elongate, 1–9 cm long, 8–32-flowered; floral bracts <11 mm long; leaves bullate; calyx and corolla densely pubescent with short curly hairs; calyx lobes lacerate-glandular ..... *C. talamancensis*
- 9a. Calyx lobes broadly overlapping over entire length at anthesis; floral bracts appressed to flowers, persistent in fruit ..... *C. confertiflora*
- 9b. Calyx lobes not overlapping at anthesis, rarely contiguous at base; floral bracts spreading, deciduous in fruit ..... 10
- 10a. Base of calyx tube distinctly apophysate ..... *C. limonensis*
- 10b. Base of calyx tube rounded or truncate, not apophysate ..... 11
- 11a. Calyx lobes oblong, apically rounded, marginally wavy, imbricate in bud, overlapping after anthesis (rarely contiguous at base during anthesis) ..... *C. calycina*
- 11b. Calyx lobes triangular, apically acute (rarely obtuse), valvate in bud, sometimes overlapping after anthesis ..... 12
- 12a. Calyx densely woolly, the matted hairs persistent; leaf blades persistently soft-pilose beneath ..... *C. pubescens*
- 12b. Calyx glabrous to pilose but never woolly, the hairs never matted; leaf blades glabrous to pubescent beneath ..... 13
- 13a. Corolla (10) 14–23 (28) mm long, terete or nearly so; floral bracts flat or slightly concave, (11) 17–30 (40) mm long, ascending or slightly spreading; leaf blades usually flat, glabrous to pubescent; corolla dark pink to red with white tip; plants without odor of wintergreen .. *C. bracteata*
- 13b. Corolla 6.5–11 (13) mm long, conspicuously bluntly angled; floral bracts conduplicate-keeled, 10–25 mm long and ascending; leaf blades usually conspicuously bullate, glabrous; corolla orange with white tip; plants with odor of wintergreen ..... *C. quereme*
- 14a. (From 2b) Leaf blade apex rounded, obtuse, or rarely subacute to acute; corolla <15 mm long; calyx tube and pedicel usually long-pilose, the sinuses usually ciliate; calyx lobes with intermittent, glandular thickenings which may coalesce at apex ..... *C. quercina*
- 14b. Leaf blade apex acuminate to caudate-acuminate, or rarely acute; corolla usually >15 mm long;



- calyx tube, pedicel, and sinuses usually glabrous (hirsute in *C. herrerae*); calyx lobes either completely callose-thickened, or with very distinct marginal thickenings ..... 15
- 15a. Floral bract margins, bracteole margins, pedicels, rachises, and usually calyx tube with red, globular or peltate glands; leaf blades with pustular or globular glands along upper surface and margin (these sometimes caducous or obscure, but leaving scars) ..... 16
- 15b. Plants lacking red, globular, peltate, or pustular glands (*C. endresii* may have several flesh-colored, angular glands at top of pedicel) ..... 23
- 16a. Leaf blades linear-lanceolate to linear-elliptic, ca. 9 times longer than broad; bracteoles 27 mm long, just beneath calyx ..... *C. pseudostenophylla*
- 16b. Leaf blades elliptic, lance-elliptic or ovate-lanceolate, less than 4 times longer than broad; bracteoles <15 mm long, at base or middle ..... 17
- 17a. Calyx tube conspicuously apophysate at base ..... 18
- 17b. Calyx tube at most inconspicuously apophysate at base ..... 20
- 18a. Rachis 1–1.5 mm diam. at base, glabrous, 4–7 (10)-flowered; floral bracts lance-elliptic to oblong-lanceolate, apically acuminate, 7–11 (16) mm long; bracteoles oval to semi-orbicular, 1–4 mm long; corolla glabrous ..... *C. lactiviscida*
- 18b. Rachis 1.2–3 mm diam. at base, moderately to densely hirsute, 14–29-flowered; floral bracts oblong to obovate, apically rounded to acute, (11) 17–26 mm long; bracteoles ovate to oblong-ovate; corolla pilose toward apex (corolla not seen in *C. herrerae*) ..... 19
- 19a. Rachis 6–8 cm long, densely hirsute; bracteoles ovate, 1–1.5 mm long; calyx tube glabrous; calyx lobes completely callose-glandular ..... *C. ciliata*
- 19b. Rachis 10–11 cm long, moderately hirsute; bracteoles oblong-ovate, 4–6 mm long; calyx tube hirsute; calyx lobes only marginally glandular ..... *C. herrerae*
- 20a. Rachis 1.5–10.5 cm long (usually <5 cm long) and ca. 1–1.5 mm diam., 6–12-flowered; bracteoles linear ..... 21
- 20b. Rachis usually >8 cm long and 3–5 mm diam., 11–26-flowered; bracteoles ovate to lanceolate or oblong-oblongate ..... 22
- 21a. Leaf blades flat; rachis 1.5–4.5 cm long; bracteoles linear to linear-lanceolate; corolla pilose in apical  $\frac{1}{3}$  ..... *C. chiriquiensis* var. *chiriquiensis*
- 21b. Leaf blades bullate; rachis (2.5) 6–10.5 cm long; bracteoles ovate to oblong-ovate; corolla glabrous or only weakly puberulous in apical  $\frac{1}{3}$  ..... *C. chiriquiensis* var. *bullata*
- 22a. Bracteoles 12–14 mm long, at middle of pedicel, concealing all calyx and lower part of corolla at anthesis ..... *C. fortuneensis*
- 22b. Bracteoles 1.5–2 (4) mm long, basal, never concealing calyx or corolla ..... *C. panamensis*
- 23a. Calyx lobes glandular callose-thickened only along margin ..... 24
- 23b. Calyx lobes usually completely glandular callose-thickened (sometimes glandular only in apical  $\frac{2}{3}$  in *C. subfasciculata*, rarely just marginally in *C. megabracteata*) ..... 25
- 24a. Leaf blades linear ..... *C. linearifolia*
- 24b. Leaf blades ovate or ovate-elliptic ..... *C. osaensis*
- 25a. Floral bracts apically rounded, usually deeply emarginate ..... 26
- 25b. Floral bracts apically acute to rounded, never emarginate (apiculate and rarely emarginate in *C. melastomoides*) ..... 27
- 26a. Corolla 31–40 (43) mm long, the lobes never glandular-callose; floral bracts (20) 30–60 (70) mm long, dark red in bud but turning pink or pale purplish-red at anthesis; calyx 7–11 (13) mm long, the limb cylindric to slightly spreading ..... *C. megabracteata* var. *megabracteata*
- 26b. Corolla 20–24 (30) mm long, the lobes sometimes glandular-callose; floral bracts (15) 20–30 (40) mm long, greenish to pinkish-green at anthesis; calyx 5–7 (10) mm long, the limb campanulate to cylindric ..... *C. subfasciculata*
- 27a. Rachis (0.7) 1–2 (3) cm long, 3–8-flowered; pedicel <10 mm long, apically with several large, flesh-colored, angular glands; bracteoles essentially completely glandular callose-thickened ..... *C. endresii*
- 27b. Rachis (2) 3–12 cm long, (4) 6–40-flowered; pedicel usually 10 mm long or more, lacking large angular glands; bracteoles glandular callose-thickened only in apical  $\frac{2}{3}$ – $\frac{1}{3}$  ..... 28

- 28a. Rachis 1–1.5 mm diam. at base; floral bracts 4–22 mm long, 3–12 mm wide ..... 29
- 28b. Rachis (1.7) 2–5 (10) mm diam. at base; floral bracts (15) 20–40 (60) mm long, (7) 10–25 (35) mm wide ..... 31
- 29a. Corolla 16–20 mm long, white; Cordillera de Tilarán, 950–1500 m ..... *C. melastomoides* var. *albiflora*
- 29b. Corolla (19) 26–41 mm long, reddish-maroon or blue; Cordillera Central–Cordillera de Talamanca, (1050) 1400–2800 m ..... 30
- 30a. Rachis and pedicels usually densely glandular-fimbriate; floral bracts apically rounded or acute; bracteoles lanceolate or narrowly ovate-lanceolate, glandular-callose in apical  $\frac{1}{3}$ – $\frac{1}{2}$ ; corolla reddish-maroon; Costa Rica ..... *C. melastomoides* var. *melastomoides*
- 30b. Rachis and pedicels with at most few, scattered, glandular fimbriae; floral bracts apically slightly notched and callose-apiculate; bracteoles broadly ovate to semi-orbicular, callose-apiculate; corolla blue; Panama ..... *C. melastomoides* var. *coloradensis*
- 31a. Rachis and pedicels with minute, scattered, reddish, globular or clavate glands along entire length; calyx tube apophysis merely undulate at base; floral bracts usually caducous; corolla whitish to purplish-rose; bracteoles usually conspicuously 3–5-nerved ..... *C. wercklei*
- 31b. Rachis and pedicels essentially eglandular; calyx tube apophysis usually deeply lobed at base; floral bracts persistent through anthesis; corolla white with purple-margined lobes or purple to lavender; bracteoles not conspicuously nerved ..... 32
- 32a. Corolla densely sericeous (rarely glabrous), white (only lobe margins purple); floral bracts pink; rachis 4–12 cm long, 15–40-flowered; petioles densely pilose to glabrate ..... *C. callista*
- 32b. Corolla short-pilose over entire length or only in apical half, purple; floral bracts deep violet or lavender- to maroonish-purple; rachis 3–8 (9) cm long, (7) 11–20 (30)-flowered; petiole glabrous even when young. .... *C. atrovioleacea* var. *atrovioleacea*

**Cavendishia atrovioleacea** Luteyn var. **atrovioleacea**, Brittonia 28: 49. 1976. Illustration: J. L. Luteyn, Mem. New York Bot. Gard. 28(3): 121, fig. 68. 1976. Figures 11 and 12.

Epiphytic, sometimes scrambling **shrubs**, 1–3 m tall. **Leaves** with petioles (4) 6–15 mm long, glabrous; leaf blades lanceolate to lance-elliptic, rarely oblanceolate or ovate, (3) 8–15 (18) cm long, 1–5 (6) cm wide, base rounded, obtuse, cuneate, or rarely subtruncate, apex acuminate, rarely  $\pm$  bullate, (3) 5 (7)-plinerved, midrib inconspicuously raised in basal 1–2 cm, essentially glabrous. **Inflorescences** fusiform to cylindric, (7) 11–20 (30)-flowered; rachis 3–8 (9) cm long, 2–5 mm diam., glabrous; floral bract oblong to oblanceolate, 20–40 (50) mm long, glabrous, deep violet to maroonish-purple, often appearing black, rarely translucent; pedicels (6) 9–13 (16) mm long, glabrous; bracteoles at or near base, lanceolate to linear-lanceolate rarely ovate, 1–4 (5.5) mm long, apex glandular-callose. **Flowers** with calyx 5.5–11 (13.5) mm long, glabrous, tube cylindric, coarsely 10-ribbed, (2) 2.5–4 (5.5) mm long, apophysate at base with rim deeply 5-lobed, limb cylindric or somewhat spreading, 3–8 mm long, weakly ribbed or minutely papillate, lobes 1–2 (2.5) mm long, triangular, erect after anthesis, margins glandular-callose, sinuses obtuse to concave; **corolla** cylindric, thinly carnosose when fresh, sometimes translucent, 20–38 (45) mm long, 5–8 mm diam., short-pilose over entire length or only in apical half, sometimes viscid puberulent, whitish-purple at base, purple to dark purple or lavender elsewhere, lobes oblong, obtuse, 1.5–2 mm long; **stamens** 19–39 mm long; filaments alternately 3.5–6 mm

and 7–14.5 mm long, subglabrous or moderately pilose; anthers alternately 18–35.5 mm and 13–27.5 mm long, thecae 6–13.5 mm long. **Berry** not seen.

*Cavendishia atrovioleacea* is endemic to Costa Rica and western Panama, where it is found in cloud forest, in *Chusquea*–*Quercus* forest, in wet forest, along stream banks, and rooted in remnant trees in pastured areas, (150) 400–2600 m elevation. It is common on the western side of Volcán Barú, Chiriquí Province, Panama, at elevations of 1300–2500 m but has also been collected about a dozen times from scattered localities in Costa Rica from extreme eastern Puntarenas Province (Cordillera de Talamanca, Cerro Pando, 1860 m) and Limón Province (Cordillera de Talamanca, Atlantic slopes, near border with Panama, 2200–2600 m), to Cartago Province (Cantón Turrialba, Atlantic watershed, 1200 m), to Alajuela Province (Cordillera Central, Laguna Hule road, 400–900 m), and as far west as Guanacaste Province (Cordillera Tilarán, Monteverde region, 700–900 m). Flowering specimens have been collected in May–September; fruiting in January and October. **Endangered.**

*Cavendishia atrovioleacea* is characterized by its large, deep violet to maroonish-purple floral bracts; many-flowered elongate inflorescences; conspicuously apophysate and deeply lobed calyx

tube base; and glandular-callose calyx lobes. The lower elevation collections from Alajuela Province differ from other collections by slightly shorter corollas and more bullate leaf blades. Variety *foliosum* Luteyn is a rare endemic to the low, Continental Divide forests of central Panama (Coclé and Colón Prov.). It differs from the nominal variety primarily by its shorter corollas and much more prominent leaf blade midrib. *Cavendishia atrovioleacea* belongs to sect. *Callista*, which in Costa Rica/Panama is a closely knit group of species of *Cavendishia* characterized, in general, by plinerved leaves, large floral bracts and corollas, and strongly apophysate calyces that are usually conspicuously lobed or ribbed (Luteyn, 1983). It is difficult to say which species are more closely related because each has its own derived features. *Cavendishia atrovioleacea* is most closely related to the widespread *C. callista*, with which it may also hybridize where their ranges overlap; one collection especially, Luteyn *et al.* 15241 from Guanacaste Province (Monteverde region), appears intermediate between these two species. More collections of this rare species are needed, especially from the Alajuela Province area, before the exact limits of its variation in Costa Rica are known.

***Cavendishia axillaris*** A. C. Smith, Contrib. U.S. Natl. Herb. 28: 493. 1932. *Cavendishia gautherioides* A. C. Smith, Ann. Missouri Bot. Gard. 28: 444. 1941. Illustrated: J. L. Luteyn, Mem. New York Bot. Gard. 28(3): 98, fig. 45. 1976. J. L. Luteyn, Fl. Neotrop. Monogr. 35: 168, fig. 57E–H. 1983. Figure 11.

Terrestrial or epiphytic **shrubs** 0.5–1.5 (3) m tall, sometimes lianoid, glabrous when mature. **Leaves** with petioles 1.5–3 (5) mm long; leaf blades hard, brittle, bullate, ovate, obovate, elliptic or suborbicular, 4.5–10.5 (17) cm long, (2.5) 4–11 cm wide, base cuneate, obtuse or rounded and subcordate then often slightly amplexicaul and clasping, apex obtuse or rounded, pinnately veined. **Inflorescences** solitary or rarely 2–5 per axil, capitate to cylindric, tightly congested, (5) 9–15 (47)-flowered; rachis 1–2 (8) cm long; floral bract concave, often persistent, striate, obovate to semi-orbicular, appressed to and concealing calyx and lower portion of corolla at anthesis, 7–10 (13) mm long, pink to dark rose-red, margin densely glandular-fimbriate; pedicels to 1 mm long; bracteoles similar to floral bract, but (5) 7–9 mm long. **Flowers** with calyx (4.5) 6–7.5 mm long, tube cylindric, smooth to rugose, (1.5) 2.5–3 mm long, limb spreading to campanulate, (2.5) 3.5–4 (5) mm long, conspicuously striate, lobes 1–2 mm long, ovate, triangular or rarely oblong, erect after anthesis, margin glandular-fimbriate, sinuses acute or narrowly obtuse; **corolla** cylindric to bottle-shaped, (6.5) 9–10 mm long, 3.5–

4 (6) mm diam., often glandular-fimbriate apically, white to pale green in basal  $\frac{1}{3}$ , green to yellowish-green in middle  $\frac{2}{3}$ , the narrowed throat and lobes pale green, lobes oblong to narrowly triangular, obtuse, 1–2 mm long; **stamens** 6–8.5 mm long; filaments alternately 1.5–2.5 mm and 2.5–3.5 mm long, short-puberulent apically; anthers alternately 5–6.5 mm and 4–6 mm long, thecae 1.5–2.5 mm long. **Berry** spherical, 9–10 mm diam., purple to blue-black.

*Cavendishia axillaris* occurs in cloud forest, elf-in forest, tropical wet forest, remnant trees in pastureland, and fence-row trees and along disturbed roadside slopes, 550–2700 m elevation. It is common from Alajuela Province (Cordillera Tilarán), Costa Rica, through Coclé Province, Panama, and then infrequently along the Panama/Colombia border and into northern Colombia (NW Antioquia Dept.); one collection has been made in southern Nicaragua. Flowering occurs throughout the year; fruiting specimens have been collected in March, April, June, July, November, and December. **Widespread.**

*Cavendishia axillaris* is morphologically very uniform throughout its range, being characterized by pinnately veined, often strongly bullate leaf blades that are subsessile and often very hard/brittle-coriaceous, densely compact inflorescences, floral bracts and bracteoles that are conspicuously nerved (sclerified), pinkish, and tightly appressed to the calyx, and small and pale green to yellowish-green corollas. *Cavendishia axillaris* belongs to ser. *Cavendishiae*, although it is morphologically similar to *C. complectens* (ser. *Imbricatae*), with which herbarium specimens have sometimes been confused. Both species have pinnately veined leaf blades and rather compact inflorescences, although the rachis of *C. complectens* may lengthen considerably after anthesis. They are most easily distinguished by the amplexicaul leaves and reniform and broadly imbricate calyx lobes of *C. complectens* (the leaves of *C. axillaris* are merely subsessile or rarely clasping and the calyx lobes usually triangular to ovate and only very rarely imbricate at the base). *Cavendishia axillaris* may hybridize with *C. complectens* and *C. quereme* since there are plants with intermediate morphologies (Luteyn, 1976c). A common name in Alajuela Province for *C. axillaris* is *el macho*. The species is visited by hummingbirds (pers. observ.).

***Cavendishia bracteata*** (Ruiz & Pav. ex J. St.-Hil.) Hoerold, Bot. Jahrb. Syst. 42: 280. 1909. *Thibaudia bracteata* Ruiz & Pav. ex J. St.-Hil.,

Expos. Fam. Nat. I: 363. 1805. *T. crassifolia* Benth., Pl. Hartw. 65. 1840. *Polyboea crassifolia* (Benth.) Klotzsch, Linnaea 24: 31. 1851. *Proclesia warszewiczii* Klotzsch, Linnaea 24: 35. 1851. *C. crassifolia* (Benth.) Hemsl., Biol. Centr.-amer., Bot. 2: 273. 1881. *C. latifolia* Hemsl., Biol. Centr.-amer., Bot. 2: 273. 1881. *C. warszewiczii* (Klotzsch) Hemsl., Biol. Centr.-amer., Bot. 2: 273. 1881. *Chupalon crassifolia* (Benth.) Kuntze, Rev. Gen. Pl. 2: 383. 1891. *Chupalon latifolium* (Hemsl.) Kuntze, Rev. Gen. Pl. 2: 383. 1891. *Chupalon warszewiczii* (Klotzsch) Kuntze, Rev. Gen. Pl. 2: 383. 1891. *Cavendishia costaricensis* Hoerold, Bot. Jahrb. Syst. 42: 326. 1909. *Cavendishia hoffmannii* Hoerold, Bot. Jahrb. Syst. 42: 328. 1909. *Cavendishia smithii* Hoerold, Bot. Jahrb. Syst. 42: 328. 1909. *Cavendishia skutchii* A. C. Smith, J. Washington Acad. Sci. 27: 308. 1937. Illustration: J. L. Luteyn, Mem. New York Bot. Gard. 28(3): 108, fig. 55. 1976 (as *Cavendishia crassifolia*). J. L. Luteyn, Fl. Neotr. Monogr. 35: 144, fig. 53. 1983. Figures 10, 11, and 14.

Terrestrial or epiphytic **shrubs** 1–3 m tall; mature stems glabrous to pilose. **Leaves** with petioles (3) 5–11 (17) mm long, glabrous to pilose; leaf blades oblong, elliptic or ovate, (2.5) 4–15 (22) cm long, (1) 1.5–5 (11) cm wide, base rounded, cordate, cuneate or subtruncate, apex acute to acuminate, often abruptly, glabrous or pilose along veins above and below, (3) 5–7 (9)-plinerved. **Inflorescences** capitate and congested or elongate-cylindric and loosely flowered, (4) 6–20 (40)-flowered; rachis (0.5) 1–5 (8) cm long, glabrous to pilose, sometimes glandular-fimbriate; floral bract oblong, ovate, elliptic, or oblanceolate, flat or slightly concave, (11) 17–30 (40) mm long, ascending or slightly spreading, glabrous to pilose, pink to dark red, sometimes glandular-fimbriate; pedicels (1.5) 6–15 (20) mm long, glabrous or pilose, often glandular-fimbriate; bracteoles usually basal, ovate to linear, rarely aristate, 1–4 mm long, glabrous to pilose, sometimes glandular-fimbriate. **Flowers** with calyx (3.5) 4–6 (9) mm long, glabrous to pilose, often glandular-fimbriate, calyx tube cylindric, smooth or somewhat rugose, often pentagonal, 1.5–3 (4) mm long, limb cylindric to campanulate, usually somewhat spreading, (1.5) 2–3 (6) mm long, lobes (0.5) 1–2 (3) mm long, triangular, connivent after anthesis, margin glandular-fimbriate, fimbriae sometimes fused, sinuses concave or acute; **corolla** cylindric to bottle-shaped, terete or broadly angled, (10) 14–23 (28) mm long, 4–5 mm diam., glabrous to pilose, sometimes glandular-fimbriate, dark pink to red, lobes deltate, 1–2 mm long, white; **stamens** 11.5–19 mm long; filaments alternately 2–4 mm and 3.4–6.5 mm long, glabrous or pilose; anthers alternately 10–16.5 mm and 7.5–14.5 mm long, thecae 2.5–6 mm long. **Berry** 8–14 mm diam., spherical, blue-black, glabrous or pilose.

*Cavendishia bracteata* occupies montane for-

est, *Chusquea-Quercus-Comarostaphylis* forest in Costa Rica or secondary growth, bogs, thickets, and rocky roadside slopes, (300) 1000–3200 m elevation. It is distributed from Mexico to Bolivia. Flowering and fruiting occur throughout the year. **Common.**

*Cavendishia bracteata* is the most frequently encountered species of *Cavendishia* (and probably Ericaceae as a whole) in Costa Rica. It is especially showy in the Cordillera de Talamanca, south along the PanAmerican Hwy. above Cartago starting at about 1500 m elevation. It is characterized by having a nonapophysate calyx tube that is longer than the limb, glandular-fimbriate calyx lobes, and bright red corollas with white lobes. Because of its extensive geographical range, *C. bracteata* has many local populations that are highly variable morphologically, as is also indicated by its long list of synonyms just for Costa Rican material.

*Cavendishia bracteata* belongs to ser. *Cavendishiae*, and it is most closely related to *C. pubescens*, a species not yet found in Costa Rica but common in western Panama's Chiriquí Province along the western slopes of Volcán Barú to within a few kilometers of the border with Costa Rica. With more intensive collecting near the border, *C. pubescens* will almost certainly be found within Costa Rica. *Cavendishia pubescens* may be easily distinguished from *C. bracteata* by its persistently and softly, short-puberulent leaf undersurfaces (not glabrous or pilose to glabrate); calyces with woolly, matted pubescence (not glabrous or pilose); calyx limbs that are longer than the tubes (not shorter); corollas that are densely short-pilose and thin and soft in texture (not glabrous to densely pilose and coriaceous and waxy-nitid); and densely puberulent (not glabrous to pilose) berries. *Cavendishia bracteata* may hybridize with *C. endresii*, *C. capitulata*, and *C. pubescens* based on morphologically intermediate collections (Luteyn, 1976c). Common names for *Cavendishia bracteata* in Costa Rica include *arrayán*, *colmillo*, and *San Miguel*.

In Costa Rica, the hummingbirds *Eugenes fulgens spectabilis*, *Lampornis calolaema*, and *Panterpe insignis* forage populations of *C. bracteata* for nectar and probably pollinate it in the process (pers. observ.; Colwell, 1973; Luteyn, 1998). The flower-piercer *Diglossa plumbea* also visits *C. bracteata* to rob nectar (Colwell, 1973, as *Cavendishia smithii*), which is the reason for the small holes often seen at the base of the corolla.

**Cavendishia callista** J. D. Smith, Bot. Gaz. 20: 5, pl. II. 1895. *C. longiflora* J. D. Smith, Bot. Gaz. 37: 420. 1904. *C. bullata* A. C. Smith & Standl., Contrib. U.S. Natl. Herb. 28: 453. 1932. Illustration: J. L. Luteyn, Mem. New York Bot. Gard. 28(3): 120, fig. 67. 1976. J. L. Luteyn, Fl. Neotrop. Monogr. 35: 262, fig. 77. 1983. Figures 11 and 14.

Terrestrial and epiphytic **shrubs** 1.5–3 m tall; mature stems glabrate or persistently pilose; twigs pinkish to flesh-colored and glaucous, glabrous to pilose-hispid. **Leaves** with petioles (4) 6–13 (22) mm long, glabrous to densely pilose; leaf blades ovate, elliptic, oblong or rarely obovate, (4.5) 7–23 (35) cm long, (1) 2.5–10 (13) cm wide, base obtuse, rounded or truncate, often cordate, apex acute to acuminate, sometimes abruptly short-acuminate, glabrous to pubescent on lamina above, glabrous or densely hispid beneath, often scabrous, (3) 5 (9)-plinerved, often strikingly bullate. **Inflorescences** elongate-cylindric, 15–40-flowered, viscid; rachis stout, 4–12 cm long, ca. 4–5 mm diam., glabrous or sericeous; floral bract oblong, obovate, or oblanceolate, (15) 20–47 (60) mm long, 10–20 (30) mm wide, glabrous, pink to deep rose; pedicels 6–15 (20) mm long, glabrous to sericeous; bracteoles basal to submedial, 1–5 (8) mm long, apex glandular-callose, usually glabrous. **Flowers** with calyx 5–9 (11) mm long, glabrous or infrequently pilose-hispid, tube cylindric, (1.5) 2–4 (5.5) mm long, coarsely ribbed, rugose, often muricate, strongly apophysate at base, limb cylindric or spreading to campanulate, 3.5–6 (8) mm long, smooth or striate, often muricate, lobes 1–2.5 (4) mm long, triangular, erect after anthesis, green, glandular-callose, sinuses obtuse to broadly acute; **corolla** cylindric, (15) 18–30 (42) mm long, 4–8 mm diam., densely sericeous (rarely glabrous), white to pearl-white or with a pinkish hue, lobes white with purple margins; **stamens** (13) 18–34 mm long; filaments alternately (1.5) 3–4.5 (6) mm and (4.5) 6–12 mm long, distinct or weakly coherent at base; anthers alternately (11) 16–32 mm and (8.5) 12–26 mm long, thecae 5–20 mm long. **Berry** spherical, 8–13 mm diam., purple to blue-black.

*Cavendishia callista* is found primarily in cloud forest, woods, and disturbed roadsides, 200–2000 m elevation. It is distributed in Guatemala, Nicaragua, Costa Rica, central Panama, Colombia, Ecuador, the Guianas, and Brazil. Flowering specimens have been collected from December through August but vary locally; fruiting in April–August. **Widespread.**

*Cavendishia callista* is characterized by having twigs that are pinkish to flesh-colored and glaucous; often strikingly bullate leaf blades, rose-pink colored floral bracts, rachis, pedicels, and calyx; elongate rachis; conspicuously ribbed and apophysate calyx tube; calyx lobes that are green and glandular-callose thickened; and corollas that are densely sericeous (rarely glabrous) and pearl-

white with purple-margined lobes. In leaf morphology and leaf and stem pubescence, *C. callista* is highly variable, but the above combination of features characterizes the species. It is one of the most beautiful cavendishias in Costa Rica. Within Mesoamerica and *Cavendishia* sect. *Callista*, *C. callista* is most closely related to *C. atrovioleacea* and *C. wercklei* based on inflorescences many-flowered, floral bracts large and apically acute, obtuse, or rounded (never emarginate); rachises elongate, thick and stout; pedicels usually >10 mm long and lacking apical angular glands; and bracteoles glandular apically (not completely). It may be distinguished from *C. wercklei* by its eglandular rachis and pedicels and from *C. atrovioleacea* by its usually sericeous, white corollas (not short-pilose and purple). A common name in Costa Rica is *colmillo de perro*. The species is visited by hummingbirds (pers. observ.).

**Cavendishia calycina** A. C. Smith, Ann. Missouri Bot. Gard. 28: 447. 1941.

Terrestrial or epiphytic **shrubs** to 5 m tall; mature stems subterete, smooth to slightly striate, glabrous; twigs subterete or bluntly angled, striate or ridged, glabrous. **Leaves** with petioles subterete, flattened adaxially, rugose, 4–7 (13) mm long, 1–3 mm diam., glabrous, blade sometimes narrowly decurrent along upper  $\frac{1}{3}$  causing it to appear slightly winged; leaf blades thin to thick-coriaceous, lanceolate, elliptic, ovate- or oblong-elliptic, 6–17.5 cm long, 2–6.5 cm wide, base broadly cuneate or rounded, apex long-acuminate, glabrous, 5–7-plinerved from near base, midrib raised and thickened in basal 1.5 cm, then impressed above, raised and prominent beneath, lateral nerves impressed or becoming plane apically above and prominent beneath, reticulate veinlets impressed or slightly raised above and inconspicuous beneath or conspicuously elevated beneath and then leaves appearing slightly bullate. **Inflorescences** capitate-globose and (6) 8–10-flowered or elongate-cylindric and 10–40-flowered, with numerous, imbricate, coriaceous, smooth, glabrous to densely appressed pilose, broadly ovate to oblong-ovate bracts to 20 mm long at base; rachis subterete, bluntly angled, rugose, 1.5–20 cm long (but still in bud), 3–4.5 mm diam., glabrous, nodes congested or widespread; floral bract chartaceous to membranaceous, oblong-elliptic, 20–36 mm long, 16–25 mm wide, apex rounded, glabrous, pink; pedicels slightly rugose, 3–10 (13) mm long, 1–2 mm diam., glabrous; bracteoles basal, chartaceous, oblong or ovate-oblong, keeled, slightly auriculate, 4–8.5 mm long, (1.5) 3–5 mm wide, apex rounded, margin glandular-fimbriate and broadly scarious. **Flowers** with calyx 7–15 mm long, glabrous, tube cylindric or somewhat campanulate, slightly rugose, 1.5–3 mm long, basally rounded but shallowly undulate, bearing glandular fimbriae, limb cylindric somewhat spreading, 5.5–11 mm long, bearing scattered glandular fimbriae, lobes oblong, 3–8 mm long, 1.5–4 mm wide,

apex rounded and apiculate, margin undulate, broadly scarious and glandular-fimbriate, separate at anthesis but imbricate in bud and after anthesis when then erect and curling around base of style; **corolla** cylindric or bottle-shaped, slightly carnos, 18–31 mm long, ca. 5–7 mm diam., glabrous, dark pink to red, lobes deltoid, ca. 1–1.5 mm long, widely flaring, white; **stamens** 14.5–22 mm long; filaments alternately 2.5–5 mm and 5.5–10 mm long, glabrous or densely short-pilose adaxially in apical half; anthers alternately 13–18 mm or 11–14 mm long; thecae 4–6 mm long. Mature **berry** not seen, but immature to at least 11 mm diam.

*Cavendishia calycina* is endemic to Chiriquí Province, Panama, where it is found in montane cloud forest, 1100–2200 m elevation. It has not yet been collected in Costa Rica. Flowering occurs throughout the year; immature fruits are rather more sporadic. **Locally Common.**

Based on the protologue (Smith, 1941), *Cavendishia calycina* is characterized by having a calyx limb longer than the tube, calyx lobes that are long, oblong, glandular-fimbriate, and somewhat undulate-margined and that remain erect after anthesis while curled around the style base, and by elongate, oblong bracteoles. The calyx lobes are noticeably imbricate before and after anthesis but are separate (or at best contiguous in the basal half) during anthesis. The collections from western Panama (region of Boquete) show two forms: one, like the type, has capitate-globose inflorescences with ca. 6–10 flowers; the other has elongate-cylindric inflorescences with 10–40 flowers that are characterized by an elongate rachis (4–10 cm vs. ca. 1.5 cm long) and calyx limbs (7–11 mm vs. 5–6 mm long). Until more collections are available, we have chosen not to recognize those populations with elongate-cylindric inflorescences as distinct. Because of the imbricate nature of the calyx lobes before and after anthesis, *C. calycina* may be keyed under both ser. *Cavendishiae* and *Imbricatae* in Luteyn (1983).

***Cavendishia capitulata*** J. D. Smith, Bot. Gaz. 25: 147. 1898. Illustration: J. L. Luteyn, Mem. New York Bot. Gard. 28(3): 101, fig. 48. 1976. J. L. Luteyn, Fl. Neotrop. Monogr. 35: 168, fig. 57A–D. 1983. Figure 7.

Erect, much-branched, spreading, usually epiphytic **shrubs** 0.5–1.5 (2) m tall, with twigs glabrous or densely hirsute with spreading white or yellowish trichomes 0.5 mm long, frequently also glandular-fimbriate. **Leaves** with petioles 1–3 (5) mm long, glabrate; leaf blades obovate, oblanceolate, elliptic, oblong-elliptic or ovate, 1.5–3 (6) cm long, 0.5–1.5 (3) cm wide, base cuneate or rounded, apex rounded, obtuse or rarely ta-

pering to a blunt tip, 3–5 (7)-plinerved. **Inflorescences** capitate, congested, 3–6 (7)-flowered; rachis 1–3 (7) mm long, glabrous; floral bract obovate, shallowly emarginate, 11–14 (19) mm long, glabrous, margin sparsely glandular-fimbriate, purple to reddish-purple, frequently glandular-fimbriate; pedicels (0.5) 1.5–2 (5) mm long, glabrous or pilose, rarely glandular-fimbriate; bracteoles basal, (1) 3–6 (8.5) mm long, margin densely glandular-fimbriate with fimbriae to 0.8 mm long. **Flowers** with calyx 4.5–7.5 mm long, glabrous, tube cylindric or barrel-shaped, often pentagonal, smooth or minutely rugose, 1–3 mm long and slightly apophysate at base with a narrow rim or collar, limb erect, somewhat spreading or campanulate, 1.5–4 mm long, lobes 0.5–1.5 mm long, triangular, erect or somewhat connivent after anthesis, margin glandular-fimbriate with fimbriae to 0.2 mm long, sinuses concave or obtuse, rarely acute; **corolla** cylindric, narrowed at base, constricted at apex, 10–16 mm long, 4–5 mm diam., glabrous, basal  $\frac{1}{4}$  white or pale red, middle half purple or reddish-purple, apical  $\frac{1}{4}$  plus lobes white, lobes triangular, obtuse, ca. 1 mm long; **stamens** 9–14.5 mm long; filaments alternately 1.5–3 mm and 3–6 mm long, glabrous or pubescent; anthers alternately 7.5–12.5 mm and 5.5–10 mm long, thecae 2–3 mm long. **Berry** spherical, 5–9 mm diam., purple to blue-black.

*Cavendishia capitulata* is found in tropical wet forest, premontane wet forest, montane cloud forest, thickets along roadside slopes, and remnant trees in pastureland, 350–2700 m elevation. It occurs in Costa Rica, Panama, and northern Colombia (Antioquia Dept.). Flowering occurs throughout the year; fruiting from December to July. **Widespread.**

*Cavendishia capitulata* is characterized by its small leaves that are apically obtuse or rounded; capitate, 3–4-flowered inflorescences; and corollas that are purple or reddish-purple with white lobes. When living, its leaves are often densely congested, imbricate, and point backward along the mature stems, although in size and shape there is considerable variation. In floral characters the species is very uniform. *Cavendishia capitulata* belongs to ser. *Cavendishiae* and therein is likely most closely related to *C. pilosa* Luteyn, a northern Colombian endemic (Antioquia Dept.). Although the two species ranges overlap in Antioquia, they are not sympatric. They both have similar small leaves with apex rounded or obtuse, inflorescences few-flowered, rachises short and congested, pedicels very short and apically swollen, oblong bracteoles that may extend beyond the calyces, calyx tubes basally truncate or short-rimose, and relatively short corollas. The two species are very distinct, however, and may be easily separated by *C. capitulata* being glabrous (not pilose) and having fewer flowered inflorescences

(3–7 vs. 10–12 flowers), a shorter rachis (1–7 mm vs. 1–2 cm long), and longer floral bracts (11–19 mm vs. ca. 9 mm long) that are spreading not appressed and concealing flowers. *Cavendishia capitulata* may hybridize with *C. bracteata*, based on morphologically intermediate collections (Luteyn, 1976c). The species is visited by the hummingbird *Lampornis castaneiventris calolaemus* in Costa Rica (pers. observ.; Luteyn, 1998).

**Cavendishia chiriquiensis** A. C. Smith, Ann. Missouri Bot. Gard. 28: 449. 1941. Figure 9.

Weakly erect, epiphytic shrubs to 3 m tall. **Leaves** with petioles 4–8 mm long, glabrate; leaf blades elliptic or ovate, sometimes bullate, 4.5–9 cm long, 1.5–3.5 cm wide, base cuneate, sometimes attenuate, apex long-acuminate or caudate-acuminate, glabrous or puberulous at base of midrib, 3–5 (7)-plinerved, newly unfolding leaves often with dense caducous, globular glands ca. 0.1–0.2 mm diam. on adaxial surface, these leaving minute reddish or blackish papillate scars on mature leaves. **Inflorescences** loosely 6–12-flowered, the buds with viscid, white exudate; rachis 1.5–10.5 cm long, thin, delicate, ca. 1–1.5 mm diam., sometimes flexuous, glabrous, sometimes with tiny, globular glands 0.1–0.3 (0.5) mm diam. along entire length or concentrated basally; floral bract oblong to oblanceolate, 15–16 mm long, glabrous, pink to red, margin with 11–12 sessile globular glands, to 0.5 mm diam., scattered along edge, these often caducous; pedicels 4–7 mm long, glabrous but with few globular glands and cilia apically; bracteoles basal, linear to linear-lanceolate or ovate to oblong-ovate, 1–2 (4) mm long, apex callose glandular and this deciduous, marginally with globular glands. **Flowers** with calyx 3.5–4.5 mm long, glabrous, tube cylindric or somewhat pentagonal, smooth or rugose, 1.5–2 (2.5) mm long, in-

conspicuously apophysate at base and with globular glands along margin of apophysis (not obscuring tube surface), limb campanulate to spreading-erect, rugose, ribbed, 1.5–2.5 mm long, with scattered glands similar to those on tube, lobes 0.5–1.5 mm long, triangular, sometimes apiculate, erect after anthesis, completely to only marginally glandular-callose, sinuses concave or flat; **corolla** tubular, 16–24 mm long, 4–4.5 mm diam., bluish- to reddish-purple at base, purple apically, glabrous to pilose in apical  $\frac{1}{3}$ , lobes triangular, obtuse, 1–2 mm long; **stamens** 14.5–21 mm long; filaments alternately ca. 3 mm and 5–7.5 mm long, glabrous or pilose; anthers alternately 13–20 mm and 9.5–16.5 mm long, thecae 3–6.5 mm long. **Berry** not seen.

*Cavendishia chiriquiensis* is found in the Cordillera de Tilarán and Cordillera de Talamanca of Costa Rica and Panama, 700–1900 m elevation. **Endangered.**

*Cavendishia chiriquiensis* is characterized by having an often lianoid habit, lanceolate leaf blades with long-acuminate to caudate-acuminate apices, pink to red floral bracts, apophysate calyx tube, and bluish- to reddish-purple corollas. It belongs to ser. *Lactiviscidae* and is probably most closely related to *C. panamensis*, with which it shares densely glandular-margined floral bracts and bracteoles. *Cavendishia chiriquiensis* also shows morphological similarities with *C. endresii*, both species having sometimes flexuous rachises, angular to subspherical glands at the articulation of the calyx and pedicel, and calyx lobes sometimes completely glandular thickened.

The differences between the two varieties of *Cavendishia chiriquiensis* are given in the following key:

**Key to the Varieties of *Cavendishia chiriquiensis***

- 1a. Leaf blades flat; rachis 1.5–4.5 cm long; bracteoles linear to linear-lanceolate; corolla pilose in apical  $\frac{1}{3}$  ..... *C. chiriquiensis* var. *chiriquiensis*
- 1b. Leaf blades bullate; rachis (2.5) 6–10.5 cm long; bracteoles ovate to oblong-ovate; corolla glabrous or only weakly puberulous in apical  $\frac{1}{3}$  ..... *C. chiriquiensis* var. *bullata*

**Var. *chiriquiensis*.** Illustrated: J. L. Luteyn, Mem. New York Bot. Gard. 28(3): 113, fig. 60. 1976.

**Leaves** with petioles densely white puberulous, glabrate; leaf blades flat, 3–5-plinerved, midrib, lateral nerves and veinlets impressed to slightly raised and conspicuous above, all veins raised beneath but usually only midrib conspicuous. **Inflorescence** rachis 1.5–4.5 cm long; bracteoles linear to linear-lanceolate. **Calyx tube** slightly apophysate; **corolla** pilose in apical  $\frac{1}{3}$ .

est, elfin forest, and mossy forest and along forest trails, 1800–1900 m elevation. It is distributed in Panama, on the eastern slopes of Volcán Barú, and in Costa Rica, where it is known only from Limón Province (Parq. Nac. Cord. Talamanca, Herrera & Gamboa 5993, F). Flowering specimens have been collected in December, January, and July; fruits are unknown. This variety is visited by the hummingbird *Lampornis castaneiventris castaneiventris* in Panama (pers. observ.; Luteyn, 1998).

Variety *chiriquiensis* is found in montane for-



Var. *bullata* Luteyn, Ann. Missouri Bot. Gard. 68: 157. 1981.

**Leaves** with petioles inconspicuously puberulent; leaf blades usually strongly bullate, 5–7-plinerved with midrib and lateral nerves moderately to strongly impressed above and conspicuously raised beneath, veinlets slightly raised above and usually obscure beneath. **Inflorescence** rachis (2.5) 6–10.5 cm long; bracteoles ovate to oblong-ovate. **Calyx tube** moderately to conspicuously apophysate; **corolla** glabrous or only weakly puberulous in apical  $\frac{1}{3}$ .

Variety *bullata* is found in cloud forest, along the Continental Divide in Chiriquí and Coclé Provinces, Panama, 700–1750 m elevation. In Costa Rica, it is known only from the Cordillera Tilarán in the Monteverde Cloud Forest Reserve (Haber 4705 and Haber & Bello 7376). Flowering specimens have been collected in July, August, and September; fruits are unknown.

*Cavendishia ciliata* Luteyn, Brittonia 28: 45. 1976. Illustration: J. L. Luteyn, Mem. New York Bot. Gard. 28(3): 110, fig. 57. 1976. Figure 12.

Terrestrial and epiphytic **shrubs** to 1 m tall, with twigs glabrous to weakly pilose, with tiny, spherical glands. **Leaves** with petioles 3–6 mm long, pilose; leaf blades elliptic to oblong-elliptic, (5) 11–15 (19) cm long, (2) 4–7.5 cm wide, base obtuse to rounded, apex acuminate (sometimes abruptly), glabrous but with scattered, reddish, pustular glands, 0.1–0.2 mm diam., along upper surface, hirsute beneath, 3 (5)-plinerved. **Inflorescences** cylindric, congested, 18–29-flowered, viscid; rachis 6–8 cm long, 1.5–3 mm diam., densely spreading-hirsute, also with globular glands; floral bract oblong to obovate, (11) 18–26 mm long, base auriculate, apex obtuse to rounded, margin ciliate and glandular-fimbriate, dark pink; pedicels spreading, (7) 12–16 mm long, hirsute, also with globular glands; bracteoles basal, ovate, 1–1.5 mm long, slightly pubescent, apex and margin with globular glands. **Flowers** with calyx 4.5–5.5 (7.5) mm long, tube 1.5–2.5 mm long, conspicuously apophysate at base with margin deeply 5-lobed and also bearing globular glands, limb cylindric-campanulate, 2.5–3.5 (5) mm long, basally pilose, lobes ca. 1 mm long, triangular, glabrous, erect after anthesis, completely glandular-callose, sinuses flat; **corolla** cylindric, (18) 20–21.5 mm long, 6–7.5 mm diam., swollen at base, sharply constricted and ca. 3.5 mm at throat, pilose apically, pinkish-purple but paler and almost whitened at base and apically, lobes ca. 1.5 mm long, strongly reflexed; **stamens** 14–15.5 mm long; filaments alternately 2.5–3 mm and 4–5.5 mm long, apically strigose; anthers alternately 12.5–13.5 mm and 10.5–11.5 mm long, thecae 5–5.5 mm long. **Berry** not seen.

*Cavendishia ciliata* is found in disturbed cloud forest, 1400–1700 m elevation. It is endemic to

Costa Rica and is known from only four collections in Cartago Province from the vicinity of El Muñeco and also along CR Hwy. 230 between Trinidad and Coliblanco. Flowering specimens have been collected in May–July; fruits are unknown. **Endangered.**

*Cavendishia ciliata* is characterized by having a stout, densely spreading-hirsute rachis; basally auriculate floral bracts with ciliate and glandular-fimbriate margins; a conspicuously apophysate and deeply lobed calyx tube; and calyx lobes that are glandular thickened over the entire surface. All parts of its inflorescence have the dark pink to red, globular to disc-shaped sessile glands characteristic of *C. ser. Lactiviscidae*, but it apparently has no close relatives there and cannot be confused with other members.

*Cavendishia complectens* Hemsl. var. *complectens*, Biol. Cent.-amer., Bot. 2: 272. 1881. *Chupalon complectens* (Hemsl.) Kuntze, Rev. Gen. Pl. 2: 383. 1891. Illustration: J. L. Luteyn, Mem. New York Bot. Gard. 28(3): 96, fig. 43. 1976. J. L. Luteyn, Fl. Neotrop. Monogr. 35: 118, fig. 48G. 1983. Figure 11.

Epiphytic **shrubs** to 2 m tall, sometimes subscandent (or rarely terrestrial), glabrous throughout. **Leaves** with petioles to 5 mm long; leaf blades subsessile, amplexicaul, oval to suborbicular, (5) 8–16 (18) cm long, (4) 5.5–10 (13) cm wide, base deeply cordate with lobes rounded and usually overlapping, apex obtuse to rounded, pinnately veined. **Inflorescences** loosely cylindric, usually solitary but with as many as 3 per axil, 8–80-flowered; rachis (1.2) 2–9 (20) cm long; floral bract elliptic to ovate-lanceolate, (10) 11–16 (20) mm long, smooth when fresh, often becoming ribbed when dry, ascending and often appressed at anthesis but usually spreading after anthesis, dark pink to red, margin glandular-fimbriate; pedicels (2) 4–9 (11) mm long; bracteoles similar to floral bract, (1) 3–4 (7) mm long. **Flowers** with calyx 4–10 mm long, tube hemispheric, smooth or minutely muricate, 1–3.5 (6.5) mm long, at most with a very narrow basal rim, limb cylindric or campanulate, 2.5–6.3 mm long, lobes (1.5) 2–3 (4) mm long, reniform, broadly ovate, broadly imbricate, the tips spreading at anthesis, connivent and tightly curling around base of style after anthesis, marginally glandular-fimbriate; **corolla** cylindric or bottle-shaped, 6–12 mm long, 4–6.5 mm diam., multicolored (white at extreme base then distally purplish-black, then green in midsection, then white lobes), lobes oblong, obtuse, 2–2.5 mm long; **stamens** 4.5–8.5 mm long; filaments alternately 2–3 mm and 2.7–4.3 mm long, scattered pubescent; anthers alternately 2.5–7 mm and 2.2–6.5 mm long, thecae 2–4 mm long. **Berry** spherical, 9–13 mm diam., purple to blue-black.

*Cavendishia complectens* var. *complectens* is



found in cloud or mossy forest, disturbed forest edges, remnant trees in pastureland, fence-row trees, and thickets and on weedy roadside slopes, 800–1800 m elevation. It is distributed from Nicaragua to northwestern Colombia (Chocó Dept.). Flowering and fruiting occur sporadically throughout the year. **Widespread.**

*Cavendishia complectens* is one of the easiest species of *Cavendishia* in Costa Rica to recognize because of its semi-orbicular, deeply cordate, strongly amplexicaul leaves. Variety *complectens* is widespread, whereas var. *striata* (A. C. Smith) Luteyn and var. *cylindrica* Luteyn are restricted to South America (Luteyn, 1983). *Cavendishia complectens* belongs to ser. *Imbricatae*, characterized by calyx lobes that are broadly imbricate at anthesis. Therein it is somewhat isolated, showing no apparent close relationships with any of the other species in the series. Although the inflorescences of *C. complectens* var. *cylindrica* (Colombia) closely resemble those of *C. confertiflora* in having elongate rachises, congested flowers, and persistent floral bracts (and bracteoles) that are strongly concave and tightly clasp the flowers at anthesis, this seems to be only a matter of convergence. *Cavendishia complectens* may hybridize with *C. axillaris*, some collections being morphologically intermediate (Luteyn, 1976c). *Cavendishia complectens* is visited by the hummingbird *Lampornis calolaema* in Costa Rica (pers. observ.; Luteyn, 1998).

***Cavendishia confertiflora*** A. C. Smith, *Phytologia* 1: 210. 1937. Illustration: J. L. Luteyn, *Mem. New York Bot. Gard.* 28(3): 106, fig. 53. 1976. Figure 14.

Terrestrial **shrubs** to 3 m tall, sometimes epiphytic, glabrous throughout. **Leaves** with petioles 6–10 mm long; leaf blades oblong, ovate-elliptic or oblong-elliptic, (8) 10–15 (20) cm long, (3) 3.5–5 (7) cm wide, base rounded or obtuse, apex acuminate, 5 (7)-plinerved. **Inflorescences** cylindric, tightly congested, 13–32-flowered; rachis 3–6.5 cm long; floral bract semi-orbicular to broadly oval, tightly appressed to and covering calyx and lower half of corolla at anthesis, persisting to fruit, concave, 10–17 mm long, margin glandular-fimbriate, pink to dark red; pedicels ca. 2 mm long; bracteoles basal, clasping lower half of calyx tube, 4.5–5 mm long, margin glandular-fimbriate. **Flowers** with calyx 7–9.5 mm long, glandular-fimbriate, tube obconic to hemispheric, bluntly 5-angled, slightly rugose, 2.5–3 mm long, limb erect or spreading, 4–6.5 mm long, lobes 3–5.5 mm long, imbricate at base, oblong, connivent and tightly enclosing style after anthesis, margin glandular-fimbriate; **corolla** bottle-shaped, 13–17 mm long, ca. 8 mm diam. at broadest point, dark pink at base and white

at apex, lobes oblong or triangular, ca. 1.5 mm long, white; **stamens** 9.5–11 mm long; filaments alternately 2–3 mm and 3.5–5 mm long; anthers alternately 8–9 mm and 7–8 mm long, thecae 2.5–3.5 mm long. **Berry** spherical, not seen mature, but at least 10 mm diam.

*Cavendishia confertiflora* may be found in evergreen forest, primary forest, roadside thickets, and disturbed areas, 1200–3200 m elevation. It is endemic to a small area of the Cordillera de Talamanca, north of the General Valley in San José Province, Costa Rica. Flowering specimens have been collected in January, November, and December; immature fruiting in December and January. **Locally Common.**

*Cavendishia confertiflora* is characterized by having cylindric inflorescences that are composed of many congested imbricate flowers, tightly appressed and persistent floral bracts (and usually bracteoles), and imbricate calyx lobes. It belongs to ser. *Imbricatae*, where it is morphologically most similar to *C. zamorensis* A. C. Smith, an Ecuadorean endemic. In Costa Rica, sterile material of *C. confertiflora* may be confused with *C. bracteata*, and in leaf alone it is virtually impossible to distinguish these taxa. They also share similar glands on the calyx lobes and bracteoles. *Cavendishia confertiflora* also resembles *C. calycina* (a western Panamanian endemic), both species having proportionally long calyx limbs, elongate-imbricate calyx lobes, and clasping bracteoles; none of these features, however, are well developed in *C. calycina*. The species are easily distinguished by the appressed, persistent floral bracts and tightly congested flowers of *C. confertiflora*. Plants are visited by hummingbirds (pers. observ.).

***Cavendishia davidsei*** Luteyn, *Brittonia* 48: 241, fig. 1. 1996. Figures 6 and 7.

Epiphytic **shrubs**; mature stems terete, striate to ribbed, glabrate; twigs complanate, striate to ribbed, densely short-pilose with white hairs, glabrate. **Leaves** with petioles broadly flattened and canaliculate adaxially, rugose, 3–5 mm long, densely short-hirsute, glabrate; leaf blades coriaceous, somewhat bullate, elliptic-ovate, elliptic to oblong-elliptic, rarely ovate, (2) 4–6 cm long, 1.5–2.5 cm wide, base rounded, cordate to subcordate, sometimes somewhat clasping, apex acute, obtuse to narrowly rounded, glabrous to short-hirsute at base of nerves above, moderately and persistently short-hirsute beneath, also with scattered, minute, glandular fimbriae on both surfaces, 5-plinerved from above base, midrib raised and thickened in basal 2–10 mm, then impressed apically above, conspicuously raised beneath, lateral nerves impressed above (the inner pair joined with midrib for 2–10 mm) and conspicuously raised be-

neath, reticulate veinlets slightly impressed above but conspicuously raised beneath. **Inflorescences** loosely cylindric, racemose, 8–32-flowered, surrounded at base by a series of ovate, acute bracts to 2 mm long; rachis angled, slender, striate, 3–9 cm long, densely short-pilose with white hairs; floral bract flat, elliptic, sometimes somewhat oblanceolate, 18–25 mm long, base tapering, apex acute, short-pilose on upper surface, margin glandular-fimbriate apically, pink to red; pedicels striate, 9–10 mm long, densely short-pilose, eglandular; bracteoles basal, elliptic-oblong, 2–3 mm long, apex obtuse, short-pilose, margin glandular-fimbriate. **Flowers** with calyx 4–5.5 mm long, moderately short-hirsute, tube cylindric, ribbed, 1.5–2.5 mm long, strongly apophysate basally with margin undulate to lobed, limb cylindric-campanulate, 2.5–3 mm long, lobes deltate, ca. 1.3 mm long, apex acute, eglandular, erect after anthesis, sinuses rounded; **corolla** cylindric, 11–13 mm long, ca. 4 mm diam., dark violet to purple, short-pilose, lobes erect, ovate-deltate, to 1 mm long, acute, white; **stamens** overall equal, 11–12 mm long; filaments distinct, alternately ca. 3 mm and 5.2 mm long, glabrous to weakly short-pilose; anthers alternately ca. 9 mm and 8 mm long, thecae alternately ca. 3 mm and 4.5 mm long. **Berry** not seen.

*Cavendishia davidsei* is found in montane (apparently *Quercus*) cloud forest, 2000–2600 m elevation. It is distributed in Costa Rica, where it is found on the Continental Divide of Cerro Bekom (Puntarenas-Limón Prov. border: *Davidse et al.* 25736, *Davidse & Herrera* 26204) and on Cerro Hoffman (Limón Prov., close to the border with Panama: *Davidse et al.* 28601), and Cerro Frantzius (Puntarenas Prov.: *Davidse et al.* 28552). In Panama it has been collected once in Bocas del Toro Province. It is known from a total of five collections. Flowering specimens have been collected in March and September; fruits are unknown. **Endangered.**

*Cavendishia davidsei* is distinguished by its short-pilose petioles, elongate rachis, multiflowered inflorescences, elongated floral bracts that are flat and tapering at base, eglandular pedicels, conspicuously apophysate calyx tube, calyx lobes that are erect after anthesis, short-pilose corolla, and limited geographical range. *Cavendishia davidsei* belongs to sect. *Quereme* and is morphologically similar to *C. talamancensis* and *C. gomezii*. A comparison of its important characters along with other Costa Rican members of sect. *Quereme* is given in Table 1.

**Cavendishia endresii** Hemsl., Biol. Cent.-amer., Bot. 2: 273. 1881. *Chupalon endresii* (Hemsl.) Kuntze, Rev. Gen. Pl. 2: 383. 1891. *C. glutinosa* Hoerold, Bot. Jahrb. Syst. 42: 321. 1909. Illustration: J. L. Luteyn, Mem. New York Bot.

Gard. 28(3): 116, fig. 63. 1976. J. L. Luteyn, Fl. Neotrop. Monogr. 35: 247, fig. 74A–C. 1983. Figure 9.

Terrestrial and epiphytic **shrubs** to 1–2.5 m tall, with twigs puberulent and usually also glandular-fimbriate. **Leaves** with petioles 2.5–5 (7) mm long, puberulent adaxially, rarely glabrate; leaf blades ovate, elliptic or oblong-lanceolate, (3.5) 5–8.5 (11) cm long, 1–2 cm wide, base cuneate, apex long-acuminate, pinnately veined or conspicuously (3) 5 (7)-plinerved, midrib puberulent, glabrate above. **Inflorescences** fusiform, 3–8-flowered, viscid; rachis (0.7) 1–2 (3) cm long, glabrous; floral bract oblong to oblanceolate, 15–20 (25) mm long, apex rounded to acute, margin ciliate, purple to reddish-purple; pedicels (3.5) 5–9 mm long, glabrous, but apically surrounded by flesh-colored, angular disc-shaped glands; bracteoles basal, ovate-lanceolate, 0.5–1.5 mm long, glabrous, completely glandular-callose except for small, central basal portion. **Flowers** with calyx 3–4 mm long, glabrous, tube bluntly 5-angled or -ribbed, 1–1.5 mm long, conspicuously apophysate, limb campanulate or rarely cylindric, smooth, (1.5) 2–2.5 (3) mm long, lobes 0.5–1 mm long, triangular, erect after anthesis, completely glandular-callose, sinuses concave to almost flat; **corolla** cylindric, slightly constricted at base, slightly narrowed at throat, (10) 15–20 mm long, 2.5–5 mm diam., glabrous, white at base and upper  $\frac{1}{4}$ – $\frac{1}{3}$ , purple or reddish-purple or rarely rose in middle, lobes white with purple or rose tips and margins; **stamens** 12.5–16 mm long; filaments alternately 1.5–3.5 mm and 3.5–5.5 mm long, glabrate; anthers alternately 10.5–15 mm and 8.5–12.5 mm long, thecae 2–4 mm long; style exerted at anthesis. **Berry** spherical, 10–12 mm diam., blue-black.

*Cavendishia endresii* is occasionally found in cloud forest, 1000–1700 m elevation. It is endemic to the Central Valley of Costa Rica and extreme western Panama (one collection, Chiriquí Prov.: Fortuna Dam area). Flowering specimens have been collected in February–September; fruiting specimens in May–July. **Locally Common.**

*Cavendishia endresii* is characterized by leaves that are usually pinnately veined, short rachis bearing ca. 3–8 flowers, short-ciliate floral bracts that are reddish-purple to purple in color, angular and flesh-colored pedicellar glands, almost completely glandular-callose thickened bracteoles, and purple or reddish-purple corollas with white bases and lobes. The very large, angular disc-shaped, flesh-colored glands at the top of the pedicel are diagnostic for this species.

*Cavendishia endresii* belongs to sect. *Callista*, where it has no close relatives in Mesoamerica. Instead, it is related to the Colombian *C. violacea* A. C. Smith and *C. aurantiaca* Luteyn, with which it has in common angular glands at the pedicel tips and (usually) pinnately veined leaves. *Cavendishia endresii* may hybridize with *C.*

TABLE 1. Salient morphological differences between *Cavendishia talamancensis*, *C. davidsei*, *C. gomezii*, *C. quereme*, and *C. quercina*.

	<i>Cavendishia talamancensis</i>	<i>Cavendishia davidsei</i>	<i>Cavendishia gomezii</i>	<i>Cavendishia quereme</i>	<i>Cavendishia quercina</i>
Leaves					
Petiole pubescence	Bullate Puberulent	± Bullate Hirsute	Flat Densely pilose	Bullate Glabrous	Flat Densely short-puberulent
Flowers/inflorescence	10-14	8-32	7-20	(8) 12-20 (25)	12-20 (53)
Rachis length (cm)	1-2 (4)	3-9	1-2.5	2-5 (6)	2-12
Rachis pubescence	Densely pilose	Densely pilose	Glabrous	Glabrous	Glabrous or densely hirsute
Floral bract length (mm)	8-10	18-25	12-15	10-25	(9.5) 11-18 (23)
Floral bract ribs	Present	Absent	Absent	Present	Absent
Floral bract base	Rounded, clasping	Tapering, not clasping	Tapering to obtuse, not clasping	Rounded to obtuse, slightly clasping	Rounded to obtuse, not clasping
Pedicel length (mm)	(1.5) 4.5-7	9-10	6-8	(5) 8-16 (19)	(6.5) 10-14 (18)
Pedicel pubescence	Densely pilose	Densely pilose	Glabrous	Glabrous	Sparsely to densely hirsute, rarely glabrate
Pedicel glands	Present apically	Absent	Absent	Absent	Absent
Bracteole shape	Ovate-subulate	Elliptic-oblong	Oblong-elliptic	Oblong, lanceolate or linear-lanceolate	Oblong or oblong-ovate
Calyx length overall (mm)	6-9	4-5.5	4-5	2.5-5	(5.5) 6-8 (9)
Calyx tube base	Weakly apophysate	Strongly apophysate	Strongly apophysate	Nonapophysate	Apophysate
Calyx lobes (post-anthesis)	Connivent	Erect	Erect	Connivent	Erect
Calyx sinuses (at anthesis)	Acute	Rounded	Acute	Acute	Concave
Corolla pubescence	Apically pilose	Pilose all over	Glabrous	Glabrous	Densely pilose apically, rarely glabrous

*wercklei*, *C. bracteata*, and *C. quereme* (Luteyn, 1976c). A common name around San José Province is *colmullo*. This species is visited by hummingbirds (pers. observ.).

***Cavendishia fortunensis*** Luteyn in Wilbur & Luteyn, Ann. Missouri Bot. Gard. 68: 157. 1981. Figure 1.

Epiphytic or terrestrial **shrubs**; mature stems subterete or bluntly angled, slightly striate, glabrous, with scattered pustular glands to 0.3 mm diam., reddish-brown. **Leaves** with petioles subterete, rugose, 3–5 mm long, 2.5–3.5 mm diam., glabrous or hispid only on adaxial surface, bearing globular glands 0.2 mm diam. apically; leaf blades coriaceous, bullate, lanceolate or elliptic, (5) 7–14.5 cm long, 2–5.5 cm wide, base obtuse or narrowly rounded, apex acuminate (sometimes abruptly short-caudate-acuminate), glabrous but with scattered black sessile, pustular glands 0.1 mm diam. along upper surface, these often caducous leaving a reddish punctate scar, 5 (7)-plinerved with innermost pair of lateral nerves arising 1.5 cm above base, midrib and lateral nerves deeply impressed above and conspicuously raised beneath, reticulate veinlets slightly impressed above and raised beneath. **Inflorescences** loosely cylindric, to ca. 35-flowered, lowest few nodes sterile, flowers with white, viscid exudate; rachis subterete, bluntly angled, striate, 11–25 cm long, 3–4 mm diam., glabrous, bearing scattered, globular or angular glands ca. 0.2 mm long; floral bract ovate, oblong or oval-elliptic, 21–25 mm long, 10–12 mm wide, base narrowed, truncate and clasping, apex rounded, margin crisped and bearing 12–20, dark red, globular glands, 0.1–0.2 mm diam. on each side, glabrous or weakly ciliate, pink; pedicels swollen apically, striate, 5–7 mm long, ca. 0.75 mm diam., glabrous, bearing globular glands concentrated apically; bracteoles medial, clasping or nearly concealing calyx and lower  $\frac{1}{2}$  of corolla at anthesis, oblong-oblancoate, 10–14 mm long, 6–8 mm wide, margin crisped and bearing dark red, globular glands scattered along edge. **Flowers** with calyx ca. 3.5–5 mm long, glabrous, tube cylindric, obscurely ribbed, 1.5–2.5 mm long, truncate basally, covered by globular or angular glands 0.2 mm diam., pink, limb spreading-campanulate, 2–3 mm long and covered by globular glands, lobes broadly triangular, ca. 1 mm long, erect after anthesis, completely glandular-callose in apical  $\frac{2}{3}$  and covered by globular glands, sinuses flat to concave; **corolla** thin-carnose, cylindric, slightly narrowed apically, 18–20 mm long, 4–6 mm diam., glabrous without but sparsely pilose within, pearl white to pinkish when fresh, lobes triangular, ca. 1 mm long, apex acute or obtuse; **stamens** 15–19 mm long; filaments alternately 2.5–4.3 mm and 5–7 mm long, the short ones sparsely pilose adaxially at apical tips, the long ones densely pilose adaxially in apical half; anthers alternately 14.5–17.5 mm and 11.5–15 mm long, thecae 5–8 mm long. **Berry** not seen.

*Cavendishia fortunensis* is known only from premontane cloud forest at the Fortuna Dam site in Chiriquí Province, Panama, 1100–1800 m elevation. Flowering specimens have been collected

in April and May; fruits are unknown. **Locally Common.**

*Cavendishia fortunensis* is characterized by its bullate leaves; elongate, viscid inflorescences; nonapophysate calyx tube; and abundance of globular to spherical glands. It is a typical member of ser. *Lactiviscidae* and is superficially similar to *C. albopicata* Luteyn (NW Colombia) and *C. pseudostenophylla*, the three having bracteoles medial along the pedicel. However, we feel it is more closely related to *C. panamensis* and *C. arizonensis* Luteyn (Veraguas Prov., Panama) because of its overall coarse habit, nonapophysate calyx tube, and globular to irregularly spherical glands of the calyx tube that are so abundant as to nearly obscure the surface from view. It also has in common with *C. arizonensis* bullate leaves and with *C. panamensis* bracteoles with globular glands. From these two species, *C. fortunensis* differs by the medial (not basal) insertion of the larger bracteoles (10–14 mm vs. 1.5–4 mm long) and glandular calyx limb.

***Cavendishia gomezii*** Luteyn, Brittonia 48: 244. 1996.

Epiphytic **shrubs**; mature stems terete to subterete, sometimes bluntly angled, striate, short-pilose, glabrate; twigs subterete, complanate, bluntly to sharply angled, striate, moderately short-pilose with white hairs. **Leaves** with petioles subterete, flattened adaxially, rugose, 1.7–3.3 mm long, densely short-pilose, glabrate; leaf blades coriaceous, ovate, ovate-elliptic, rarely oblong-ovate, 2–3.5 cm long, 1–1.7 cm wide, base rounded, subcordate, apex acute, obtuse, or narrowly rounded, margin slightly thickened and slightly revolute, sparsely but conspicuously short-pilose along margins and at base of midrib beneath, glabrate, also bearing deciduous, minute, glandular fimbriae on both surfaces, 3 (5)-plinerved from base, midrib plane or usually raised above and conspicuously raised beneath, lateral nerves and reticulate veinlets conspicuously raised above and slightly raised but inconspicuous beneath, sometimes only midrib noticeable beneath. **Inflorescences** cylindric, racemose, 7–20-flowered; rachis sharply angled, 1–2.5 cm long, glabrous; floral bract flat, smooth, oblong to oblanceolate, 12–15 mm long, 3–7 mm wide, base tapering to obtuse, apex rounded, eglandular, ciliate apically, red (fide label); pedicels ribbed, 6–8 mm long, eglandular, glabrous; bracteoles basal, oblong-elliptic, 2–3 (5) mm long, apex rounded to acute, margin densely and deciduously glandular-fimbriate. **Flowers** with calyx 4–5 mm long, tube cylindric, ribbed, 1.5–1.6 mm long, base broadly apophysate with the margin flaring, undulate to lobed and short-pilose, limb campanulate-spreading, 2.4–2.5 mm long, glabrous, lobes oblong-ovate, apiculate, ca. 1 mm long, margin lacerate-glandular, erect after anthesis, sinuses acute; **corolla** cylindric, 9–10 mm long, ca. 3.5 mm diam., red to vermillion, glabrous, lobes ovate, ca. 1 mm long, apex acute, white; **stamens**

equal overall, 8–8.5 mm long; filaments distinct, alternately ca. 3.5 mm and 1.5 mm long, glabrous; anthers alternately ca. 6.3 mm and 7.5 mm long, thecae alternately ca. 3 mm and 2.5 mm long; style slightly exerted, glabrous. **Berry** not seen.

*Cavendishia gomezii* is endemic to the montane cloud forest of the Cordillera de Talamanca in Bocas del Toro Province, Panama, 2400–2900 m elevation. Although having been collected four times (on one trip) close to the Costa Rican border, it has not yet been collected within the political boundaries of Costa Rica. Flowering specimens have been collected in March; fruits are unknown. **Endangered.**

*Cavendishia gomezii* is characterized by small, flat, subcordate leaf blades; essentially glabrous inflorescence parts; broadly apophysate calyx tube with the margin flaring; and lacerate-glandular calyx lobes that are erect after anthesis. It belongs to subgen. *Cavendishia* sect. *Quereme* following Luteyn (1983). In leaf size and shape and general appearance of the inflorescence, *C. gomezii* resembles *C. talamancensis*; it differs from that species by the characters mentioned in the key and Table 1. In the available collections, there is no mention of the plant having the odor of wintergreen, a general feature of sect. *Quereme*. This new species was named to honor Luis Diego Gómez, whose contributions to Costa Rican natural history have been numerous.

***Cavendishia herrerae*** Luteyn & J. F. Morales, Brittonia 48: 517. 1996[1997]. Figure 12.

Pendent, epiphytic **shrubs**; mature stems bluntly angled, striate, moderately short-hirsute, glabrate, also with scattered, globular glands ca. 0.2–0.3 mm diam.; twigs complanate, sparsely hirsute with white trichomes 0.7–0.9 mm long. **Leaves** with petioles rugose, 4–6 (7) mm long, sparsely short-hirsute, glabrate; leaf blades coriaceous, stiff, lanceolate or elliptic-lanceolate, 8–18 cm long, 1.2–3.5 cm wide, base cuneate or obtuse, apex gradually acuminate, glabrous above, sparsely hirsute along midnerve beneath, glabrate, also with few globular glands 0.1–0.2 mm diam. along margin and on blade above, 3 (5)-plinerved, midrib and inner pair of lateral nerves strongly impressed and conspicuous above, raised and conspicuous beneath, reticulate veinlets slightly impressed on both surfaces. **Inflorescences** elongate-cylindric, racemose, ca. 14-flowered; rachis striate, ribbed, 10–11 cm long, moderately hirsute and with a few, globular, sessile glands; floral bract oblong or oblong-obovate, 17–21 mm long, apex obtuse or acute, margin ciliolate and bearing few, sessile, globular glands on margin and abaxial surface, pinkish-lilac; pedicels striate, rugose, 11–14 mm long, densely hirsute, also with few, scattered, globular glands; bracteoles basal, striate, oblong-ovate, 4–6 mm long, marginally cili-

olate and also bearing few, sessile, globular glands, the tip also glandular-thickened. **Flowers** with calyx ca. 9 mm long, tube ca. 2 mm long, pink, moderately hirsute, the base apophysate, moderately undulate and bearing few, globular or disc-shaped glands, limb spreading-campanulate, ca. 7 mm long, hirsute basally, lobes triangular, ca. 2 mm long, 1.8–2 mm wide, erect after anthesis, each margin with an oblong to crescent-shaped callose gland, these contiguous at apex, sinuses acute to obtuse; **corolla** (lilac fide label) not seen; **stamens** not seen. **Berry** not seen.

*Cavendishia herrerae* is endemic to the Caribbean slope of Costa Rica (Limón Prov.). It is known only from the type specimen (Cantón de Limón, El Progreso, Valle de la Estrella, Matama ridge, trail between Cerro Muchilla and Cerro Avioneta, vic. Río Suruy, *Herrera & Chacón* 2623), which was collected in rain forest at 700 m elevation and lacked corollas. The type collection was flowering in April; fruits are unknown. **Endangered.**

*Cavendishia herrerae* is characterized by having globular glands in its vegetative and floral parts, a basally apophysate calyx tube, and glandular-margined calyx lobes. It belongs to *Cavendishia* sect. *Engleriana* ser. *Lactiviscidae*, where it is morphologically similar to *C. ciliata*. It differs from *C. ciliata* by its narrower leaf blades, leaf apex gradually (not abruptly) acuminate, longer and only moderately (not densely) hirsute rachis, shorter floral bracts that are acute (not obtuse or rounded) at the apex, larger bracteoles, hirsute (not glabrous) calyx tube and limb, calyx lobes that are callose glandular only along each margin (not the entire lobe), and its different geography and altitude. *Cavendishia herrerae* was named after Gerardo Herrera, who collected many new and interesting species of Ericaceae in Costa Rica.

***Cavendishia lactiviscida*** Luteyn, Brittonia 28: 46. 1976. Illustration: J. L. Luteyn, Mem. New York Bot. Gard. 28(3): 111, fig. 58. 1976. Figure 9.

Terrestrial or epiphytic **shrubs** to 1 m tall; mature stems and twigs with scattered, subsessile, globular glands to 0.4 mm diam., densest near nodes and on youngest branches. **Leaves** with petioles (4) 6–7 (10) mm long, hirsute, glabrate; leaf blades bullate, elliptic to lance-elliptic, 4–9 cm long, 1–3 cm wide, base cuneate, apex long caudate-acuminate (often abruptly), base of midrib above hirsute but glabrate, adaxial surface and margins of mature leaves with caducous, scattered, reddish, pustular glands 0.1–0.2 mm diam., 5-plinerved. **Inflorescences** elongate-cylindric, loosely 4–7 (10)-flowered, the basal several nodes sterile; rachis 4–9 (15) cm long, thin, 1–1.5 mm diam. at base, glabrous,

with globular glands; floral bract foliaceous, lance-elliptic to oblong-lanceolate, 7–11 (16) mm long, conspicuously nerved, pale green, apex acuminate, margin ciliate and with globular glands to 0.2 mm diam.; pedicels (14) 19–25 mm long, glabrous, with globular glands; bracteoles basal, 1–4 mm long, oval to semi-orbicular, margin glandular as floral bracts. **Flowers** with calyx 4–6 mm long, glabrous, tube short-cylindric, 10-ribbed, 1.5–2 mm long, basally apophysate with the margins undulate and bearing globular glands which secrete a milky exudate, limb erect or wide-spreading to campanulate, smooth to slightly rugose, 2.5–4 mm long, eglandular, lobes (0.5) 1 (1.5) mm long, triangular, erect after anthesis, each side with an oblong callose gland, sinuses concave to flat; **corolla** carmose with walls 1.5–2 mm thick when fresh but drying membranous, cylindric, slightly constricted at base, constricted at throat, when immature and prior to anthesis apex broadly rounded and nipple-shaped, 19–29 mm long, ca. 9.5 mm diam., glabrous, greenish-red, lobes ca. 0.5 mm long; **stamens** 15–20 mm long; filaments alternately 3.2–4.5 mm and 6.3–7.5 mm long, glabrous to weakly short-pilose; anthers alternately 12.5–17 mm and 10–14 mm long, thecae 2.5–5 mm long. **Berry** not seen.

*Cavendishia lactiviscida* is found in cloud forest, 1200–1850 m elevation. It is endemic to the Cordillera Tilarán, Costa Rica, where it has been collected fewer than 10 times. Flowering specimens have been collected in February, May, June, and July; fruits are unknown. **Endangered.**

*Cavendishia lactiviscida* is characterized by having bullate and caudate-acuminate leaf blades; loosely flowered inflorescences; foliaceous, conspicuously nerved and pale green floral bracts; long pedicels; basally undulate and apophysate calyx tube; greenish-red corollas; and globular to pustular glands scattered along mature stems, leaves, and inflorescences. Although it superficially resembles *C. chiriquiensis*, its relationships within *Cavendishia* ser. *Lactiviscidae* are obscure. The plants are visited by the hummingbird *Doryfera ludovicae* in Costa Rica (pers. observ.; Luteyn, 1998).

***Cavendishia limonensis*** Luteyn, Brittonia 48: 244, fig. 2. 1996. Figure 9.

Epiphytic **shrubs**; mature stems terete, striate, glabrous; twigs bluntly angled, striate, densely white puberulent, glabrate. **Leaves** with petioles strongly canaliculate adaxially, 4–6 mm long, densely puberulent, glabrate; leaf blades coriaceous, ovate to ovate-elliptic, 3.5–5.6 cm long, 1.2–1.8 cm wide, base rounded to broadly obtuse, apex long-acuminate, glabrous, 3 (5)-plinerved, midrib weakly impressed in basal  $\frac{1}{2}$ – $\frac{1}{3}$ , becoming plane to slightly raised in apical  $\frac{1}{2}$ – $\frac{1}{4}$ , above, lateral nerves and reticulate veinlets slightly raised above, all nerves slightly raised beneath. **Inflorescences** loosely racemose, 6–9-flowered, surrounded at base by

a series of broadly ovate bracts to 2 mm long; rachis sharply angled, 1.5–2.5 cm long, glabrous, eglandular, the basal 3–4 nodes often sterile; floral bract conduplicate or concave, oblong-obovate, 7–16 mm long, apex rounded, glabrous, eglandular, at first surrounding floral buds but becoming strongly reflexed through and after anthesis; pedicels striate, 7–10 mm long, glabrous; bracteoles basal, oblong, 1.5–2 mm long, apex rounded, glabrous, margin conspicuously glandular-fimbriate in apical  $\frac{1}{3}$ . **Flowers** with calyx 4–5 mm long, glabrous, tube cylindric, broadly and bluntly ribbed, 1.5–2 mm long, basally shallowly but distinctly apophysate, limb erect-spreading to cylindric-campanulate, 2.5–3 mm long, lobes ovate, ca. 1 mm long, erect after anthesis, margin lacerate-glandular, darker in color and apparently thinner in texture than lamina proper, sinuses acute; **corolla** cylindric, slightly narrowing at throat, 14–16.5 mm long, ca. 5 mm diam., lobes ovate-apiculate, ca. 1 mm long; **stamens** overall equal, ca. 13.5 mm long; filaments distinct, alternately ca. 4.5 mm and 2 mm long, glabrous; anthers alternately ca. 10.7 mm and 12.3 mm long, thecae alternately ca. 4.7 mm and 3 mm long. **Berry** not seen.

*Cavendishia limonensis* is found in lowland rain forest, 500–700 m elevation. It is endemic to Costa Rica (Limón Prov.), where it is known only from two collections from Cantón de Talamanca, the Alto Urén area, along the road between Quebrada Chaho and Cororíña (*Herrera 3321*) and at Cororíña, between Río Urén and Quebrada Chaho (*Fco. Solís et al. 37*). Flowering specimens have been collected in July; fruits are unknown. **Endangered.**

*Cavendishia limonensis* is characterized by its leaves that lack glandular fimbriae, petioles that are adaxially strongly canaliculate, eglandular floral bracts that are conduplicate or concave and strongly reflexed at anthesis, apophysate calyx tube, and calyx lobes with lacerate-glandular margins. It belongs to *Cavendishia* sect. *Quereme* and is most similar to *C. laurifolia* (Mexico–Guatemala, Panama–Colombia), differing by the features mentioned in Table 2.

***Cavendishia linearifolia*** Luteyn & J. F. Morales, Brittonia 48: 516, fig. 1 E–F. 1996[1997]. Figure 15.

Pendent, epiphytic **shrubs**; mature stems terete or subterete, striate, glabrous; twigs terete, glabrous. **Leaves** with petioles rugose, 1–3 mm long, glabrous; leaf blades coriaceous, linear, strongly revolute, (6) 7.5–15 cm long, 0.3–0.7 cm wide, base cuneate, apex acute, glabrous, but punctate on both surfaces from deciduous fimbriae borne in slight depressions, apparently pinnately nerved, midrib impressed above, raised and conspicuous beneath, secondary nerves obscure (if present), reticulate veinlets obscure to inconspicuous but slightly raised when present. **Inflorescences** subspherical, race-

TABLE 2. Salient morphological differences between *Cavendishia laurifolia*, *C. limonensis*, and *C. quereme*.

	<i>Cavendishia laurifolia</i>	<i>Cavendishia limonensis</i>	<i>Cavendishia quereme</i>
Leaf size (cm)	(3.5) 6–13 × (1) 2–4	3.5–5.6 × 1.2–1.8	(3.5) 6–11 (14) × (1) 1.5–4 (5)
Petiole shape	Subterete	Canaliculate adaxially	Subterete or terete
Flowers/inflorescence	(8) 17–32 (45)	6–9	(8) 12–20 (25)
Rachis length (cm)	4–15 (20)	1.5–2.5	2–5 (6)
Pedicel length (mm)	(9) 14–22 (26)	7–10	(5) 8–16 (19)
Pedicel glands	Densely glandular-fimbriate	Absent	Absent
Bracteole glands	Densely glandular-fimbriate	Glandular-fimbriate in apical ½	Glandular-fimbriate
Calyx glands	Densely glandular-fimbriate	Absent	Marginally lacerate-glandular
Calyx sinuses (at anthesis)	Flat to concave	Acute	Acute
Calyx lobes (post-anthesis)	Connivent	Erect	Connivent
Corolla length (mm)	(6.5) 8–10 (12)	14–16.5	7–11 (13)
Corolla shape (cross section)	Pentagonal	Cylindrical	Pentagonal

mose, 4–11-flowered; rachis smooth, 1–2 cm long, glabrous; floral bract obovate or oblong-obovate, 14–24 mm long, base cuneate or attenuate, apex obtuse, glabrous, dark pink when fresh; pedicels striate, sometimes rugose, 4–6 (7) mm long, glabrous; bracteoles basal, oblong, ca. 0.5 mm long, margin with 3–4 oblong, callose-fimbriae at tip. **Flowers** with calyx 6–8 mm long, glabrous, dark rose, tube smooth, 1.5–2.5 mm long, basally apophysate with margin somewhat undulate, limb tubular-campanulate, smooth to striate, 4–5.5 mm long, lobes triangular, 1.5–3 mm long, erect after anthesis, marginally glandular-thickened with 1–2 thickened fimbriae basally and these coalescing into a supramarginal gland on either side at apex, sinuses obtuse; **corolla** cylindric, narrowed at throat, 1.6–1.8 cm long, 3.5–5 mm diam., glabrous, pink, lobes erect, triangular, 1–1.5 mm long, apex acute, white; **stamens** overall equal, 13–18 mm long; filaments alternately ca. 2.5 mm and ca. 4 mm long, glabrous; anthers alternately ca. 1.7 cm and 1.5 cm long, thecae ca. 4–5 mm long. **Berry** not seen.

*Cavendishia linearifolia* is found in lowland rain forest, 100–200 m elevation. It is endemic to the Osa Peninsula of Puntarenas Province, Costa Rica, where it is known from only two collections around Golfito, along the road to Río Bonito (Herrera 5037) and along the road between Golfito and Villa Briceño (Hammel *et al.* 18398). Flowering collections have been made in January; fruits are unknown. **Endangered**.

*Cavendishia linearifolia* is characterized by its linear leaves. Only two other species of *Cavendishia*, *C. stenophylla* (endemic central Panama) and *C. pseudostenophylla* (endemic western Chiriquí Prov., Panama), have linear leaves with which it could be confused, but in both those species the leaf blade width is double that of *C. linearifolia* (1–2.5 cm vs. 0.3–0.7 cm). *Cavendishia*

*linearifolia* belongs to *Cavendishia* sect. *Engleriana* ser. *Englerianae* and is similar to *C. osaensis*, differing by its long, linear leaves; smaller bracteoles with strictly terminal glands (not scattered along entire margin); and calyx lobe glands that are more highly coalescent at the apex. More collections of both species are needed before their interspecific relationships can be more fully understood.

***Cavendishia luteynii*** J. F. Morales *in* Luteyn & Morales, Brittonia 48: 518. 1996[1997]. Figure 11.

Epiphytic **shrubs**; mature stems subterete to bluntly angled, smooth to somewhat striate, glabrous to glabrate, with scattered, globular glands ca. 0.1 mm diam.; twigs subterete, glabrous. **Leaves** with petioles inconspicuous, rugose, less than 1.5 mm long, glabrous; leaf blades coriaceous, strongly bullate, lanceolate to oblong-lanceolate, 2.4–6.8 cm long, 1.3–4.2 cm wide, base clasping to nearly amplexicaul, apex acute to scarcely mucronate, glabrous above and glabrate beneath, also with few glandular fimbriae, 5–7-plinerved, midrib and lateral nerves strongly and conspicuously impressed above and raised and conspicuous beneath, reticulate veinlets conspicuously impressed on both surfaces. **Inflorescences** elongate-cylindric, racemose, 9–18-flowered; rachis somewhat angled, striate, ribbed, 3–6 cm long, glabrous, eglandular; floral bract oblong to oblong-elliptic, 15–18 mm long, base obtuse, apex gradually acuminate, margin ciliolate, the tip callose glandular, pinkish-red to red; pedicels striate, rugose, 3–4.5 mm long, glabrous to glabrate; bracteoles basal, linear-oblong, 3.5–4.5 mm long, margin ciliolate. **Flowers** with calyx ca. 5.2–6.2 mm long, reddish, glabrous, tube ca. 2.2–2.5 mm long, basally strongly apophysate with a conspicuous collar or rim, eglandular, limb narrowly campanulate, ca. 2.5–3.5



mm long, lobes triangular, ca. 0.8 mm long, ca. 1.7 mm wide, eglandular, erect after anthesis, sinuses acute to obtuse; **corolla** cylindric, 7.5–8 mm long, ca. 2 mm diam., greenish-white to greenish-yellow, lobes erect, triangular to ovate-triangular, ca. 0.8 mm long, apex acute; **stamens** 6–7 mm long; filaments alternately ca. 1 mm and 2–2.3 mm long, glabrous to weakly short-pilose; anthers alternately ca. 5.8–6 mm and 4.5–5 mm long, thecae alternately ca. 1.8 mm and 2.7 mm long. **Berry** not seen.

*Cavendishia luteynii* is endemic to the premontane forest, 2200 m elevation, in the Cordillera de Talamanca (Limón Prov.), Costa Rica. It is known only from the following two collections: Cantón de Talamanca, Cordillera de Talamanca, Cerro Carguicacha to Cerro Biricuacua, between Ujarrás and San José Cabécar (*Herrera 6140*) and Cantón de Talamanca, Quebrada Kuisa (*J. Bittner 1820*). Flowering specimens have been collected in April; fruits are unknown. **Endangered.**

*Cavendishia luteynii* is characterized by its strongly bullate leaf blades that are basally clasping to nearly amplexicaul, short rachis, floral bracts with acuminate and callose-glandular tips, basally strongly apophysate calyx tube, and eglandular calyx lobes. It belongs to *Cavendishia* sect. *Quereme* and is related to *C. talamancensis*, differing from it by clasping to nearly amplexicaul, strongly bullate leaves; conspicuously reticulate leaf veinlets; glabrous calyx and corolla; and strongly apophysate calyx tube.

**Cavendishia megabracteata** Luteyn var. **megabracteata**, Brittonia 28: 49. 1976.

Terrestrial or epiphytic **shrubs** to 2.5 m tall, often viney in habit; mature stems terete, minutely striate, glabrous, the base to 5 cm in diam.; twigs terete to bluntly angled, striate, glabrous, reddish-brown. **Leaves** with petioles often flattened adaxially, rugose, rarely striate, 4–10 (14) mm long, 1–2.5 (3) mm diam., glabrous to densely puberulent adaxially when young, often glabrate; leaf blades ovate, lanceolate, lance-elliptic or oblong, (4) 8–12 (15) cm long, (1) 2.5–7 cm wide, base obtuse, rounded or truncate, apex acuminate and often abruptly so, often puberulous at base of midrib and lateral nerves on upper surface, 5–7-plinerved, midrib inconspicuously raised and thickened through basal 1 cm otherwise weakly impressed above, inner pair of lateral nerves moderately or weakly impressed above but sometimes plane or raised apically, outer lateral nerves and veinlets raised and usually very conspicuous above rarely impressed, all nerves raised beneath but veinlets often obscure. **Inflorescences** obconic to spherical in bud, (2) 5–9 (12)-flowered, the basal nodes often sterile; rachis coarsely and bluntly angled, striate, (0.6) 0.8–2 (3.5) cm long, ca. 2 mm diam., glabrous, rarely with clavate glands or cartilaginous teeth at base; floral bract translucent, oblong, obovate, or rarely subrotund, (2) 3–6 (7)

cm long, (1) 1.5–2.5 (4.5) cm wide, base narrowed and somewhat clasping, apex rounded, usually deeply emarginate, with minute, red, clavate, glandular fimbriae abaxially, dark red in bud but pale purplish, bright rose, or dark pink when mature; pedicels swollen apically, striate, (8) 10–16 (19) mm long, (0.5) 1 (1.5) mm diam., glabrous, rarely weakly glandular apically; bracteoles with or without prominent midrib, ovate, lanceolate, lance-elliptic, or nearly linear, 1.5–2 (5) mm long, 0.5–1.5 (4) mm wide, apex glandular-callose. **Flowers** with calyx glabrous, 7–11 (13) mm long, tube cylindric, ribbed, 2–5 mm long, 3–5 mm diam., apophysate and deeply lobed at base with lobes straight to flaring outward and extending well below articulation, limb cylindric to slightly spreading, minutely papillate, (4) 5–7.5 (9) mm long, lobes triangular, (1) 1.5–2 (2.5) mm long, erect after anthesis, tips completely glandular-callose or callose apically, centrally, or only marginally, sinuses subacute when fresh, but drying obtuse to concave, rarely flat; **corolla** cylindric, slightly constricted at base and throat, often translucent, 31–40 (43) mm long, 6–9 mm diam., glabrous or rarely pilose apically, tube dull or glossy white, often pink to pinkish at base grading through violet to pale purple apically, lobes oblong, obtuse, 1.5–2 mm long, reflexed, white sometimes marginally purple; **stamens** 24.5–36 mm long; filaments densely puberulous apically, alternately 2.5–7.5 mm and 7.5–13.5 mm long; anthers alternately 21.5–32.5 mm and 16–26.5 mm long, thecae 6–13 mm long. Immature **berry** subspherical.

*Cavendishia megabracteata* var. *megabracteata* is found in montane cloud forest, on the slopes of Volcán Barú and Cerro Horqueta, western Chiriquí Province, Panama, 1700–2500 m elevation. It has not yet been found in Costa Rica. Flowering specimens have been collected from December to August; immature fruiting specimens in January. **Endangered.**

*Cavendishia megabracteata* is characterized by its large, apically emarginate, reddish floral bracts; obconic or spherical inflorescences (when in bud); basically whitish corollas; and glandular-callose calyx lobes. Both the floral bracts and the corollas are extremely thin and translucent when dry. The size, shape, and texture of its floral bracts alone serve to distinguish this species from most other Mesoamerican species of *Cavendishia*. *Cavendishia megabracteata* is distinguished from other members of *Cavendishia* sect. *Callista* by its emarginate floral bracts (see discussion under *C. atrovioleacea*). The related *C. megabracteata* var. *attenuata* Luteyn is endemic to Coclé Province, Panama.

**Cavendishia melastomoides** (Klotzsch) Hemsl., Biol. Cent.-amer., Bot. 2: 273. 1881. *Socratesia melastomoides* Klotzsch, Linnaea 24: 23. 1851. *C. klotzschiana* Niedenzu, Bot. Jahrb. Syst. 11:



206. 1890 (nom. super.). *Chupalon melastomoides* (Klotzsch) Kuntze, Rev. Gen. Pl. 2: 383. 1891. *C. graebneriana* Hoerold, Bot. Jahrb. Syst. 42:324. 1909. Figure 9.

Epiphytic shrubs, 0.5–3 m tall; mature stems pendent, terete, smooth, glabrous, often appearing glaucous; twigs glabrous or pilose, with reddish, caducous glands. **Leaves** with petioles flattened adaxially, rugose, (3) 4.5–9 mm long, glabrous or densely short-pilose, glabrate; leaf blades ovate or elliptic, 3–8.5 (10) cm long, (1) 1.5–4 cm wide, base rounded, truncate or cuneate, apex long-acuminate or caudate-acuminate, glabrous, 3 (5)-pliner-ved, midrib impressed and prominent above becoming plane apically, raised and conspicuous beneath, lateral nerves slightly raised on both surfaces or rarely im-pressed above, obscure or conspicuous beneath, reticu-late veinlets slightly raised on both surfaces but  $\pm$  ob-scure. **Inflorescences** loosely (4) 6–10 (18)-flowered, the basal nodes often sterile, all parts viscid; rachis some-times ribbed, (2) 3–8 (15) cm long, 1–1.5 mm diam. at base, glabrous, often glandular-fimbriate; floral bract of-ten caducous, smooth or ribbed, oblong, oblanceolate or elliptic, rarely semi-orbicular, 4–22 mm long, 3–12 mm wide, apex often apiculate and glandular-callose, rarely emarginate, glandular-fimbriate, glabrous, rose to pale green, often translucent when fresh; pedicels ribbed, (7) 10–21 (27) mm long, glabrous, often glandular-fimbri-ate; bracteoles basal to medial, smooth or conspicuously nerved, ovate, ovate-lanceolate and often cochleariform or semi-orbicular, 1–5 mm long, 0.5–6 mm wide, apex glandular-thickened. **Flowers** with calyx (3) 4.5–7.5 mm long, glabrous, tube smooth or rugose, pentagonal or ribbed, 1–2 (3) mm long, with basal apophysis deeply 5-lobed and perpendicular to calyx axis, limb cylindric or somewhat spreading, often conspicuously striate, (2) 2.5–5 (6.5) mm long, lobes triangular, (0.5) 1–1.5 mm long, erect after anthesis, completely glandular-callose, sinuses obtuse or concave and almost flat; **corolla** thin-carnose, cylindric, slightly narrowed at throat, some-times curving upward apically (var. *melastomoides*), 16–41 mm long, 3–7 mm diam., viscid or not, glabrous or weakly pilose, dull white, blue or dark reddish-maroon, lobes triangular, 1–2.5 mm long, apex obtuse; **stamens** 16–34.5 mm long; filaments alternately 2.5–6 mm and 5.5–12.5 mm long, glabrous or pilose; anthers alternate-ly 14–32 mm and 11.5–25 mm long, thecae 3–8 mm

long. **Berry** spherical, 11–14 mm diam., maroon to blue-black.

*Cavendishia melastomoides* is found in Costa Rica and western Panama, 950–2800 m elevation.

*Cavendishia melastomoides* is characterized by having relatively small and narrow, acuminate leaf blades with long petioles, loosely flowered and viscid inflorescences, thin rachis, caducous floral bracts, broadly apophysate calyx tube, and maroon or white corollas. Within sect. *Callista*, *C. melastomoides* is probably most closely related to *C. wercklei* based on similarly (often) glandu-lar-fimbriate rachises and pedicels, bracteoles that are glandular-callose in the apical  $\frac{1}{3}$  to  $\frac{1}{2}$ , and often caducous floral bracts. *Cavendishia melas-tomoides* differs by its thinner rachis (1–1.5 vs. 2–4 mm diam.), smaller floral bracts (4–22  $\times$  3–12 vs. 20–30  $\times$  10–20 mm), apically curved co-rollas, and calyx tube apophysis that is deeply 5-lobed (not merely undulate) at the base. *Caven-dishia melastomoides* is separable into three mor-phologically distinct and geographically isolated varieties, vars. *melastomoides* and *albiflora* from Costa Rica and var. *coloradensis* from western Panama. Although the two Costa Rican varieties are distinguished by numerous morphological characters, perhaps indicating specific status to some, we have chosen to recognize them as var-ieties, emphasizing the features that unite them as a species rather than their differences. Al-though the differences between vars. *melastomo-ides* and *albiflora* are relatively stable, the two varieties do show some minor convergence in leaf size and shape and in corolla length and color in the area between Zarcero and Quesada (Alajuela Prov.), where their ranges meet. Nevertheless, there should be no difficulties in separating them. Both varieties are visited by hummingbirds (pers. observ.). The varieties are distinguished by the following key:

**Key to the Varieties of *Cavendishia melastomoides***

- 1a. Corolla 16–20 mm long, white; Cordillera de Tilarán, 950–1500 m ..... *C. melastomoides* var. *albiflora*
- 1b. Corolla (19) 26–41 mm long, reddish-maroon or blue; Cordillera Central–Cordillera de Talamanca, 1400–2800 m ..... 2
- 2a. Rachis and pedicels usually densely glandular-fimbriate; floral bracts apically rounded or acute, eglandular; bracteoles lanceolate or narrowly ovate-lanceolate, glandular-callose in apical  $\frac{1}{3}$ – $\frac{1}{2}$ ; co-rolla reddish-maroon; Costa Rica ..... *C. melastomoides* var. *melastomoides*
- 2b. Rachis and pedicels usually with only a few, scattered, glandular fimbriae or none; floral bracts apically rounded, slightly notched, callose-apiculate; bracteoles broadly ovate to semi-orbicular, callose-apiculate; corolla blue; Panama ..... *C. melastomoides* var. *coloradensis*

Var. **albiflora** Luteyn, Brittonia 28: 51. 1976. Illustration: J. L. Luteyn, Mem. New York Bot. Gard. 28(3): 118, fig. 65. 1976.

**Inflorescence** rachis (2) 3–4 (6) cm long, eglandular; floral bract caducous, oblong or elliptic, 4–7.5 (10.5) mm long, apex rounded and usually slightly emarginate; pedicels 9–13 (15) mm long, eglandular; bracteoles narrowly ovate-lanceolate, glandular-thickened in apical  $\frac{1}{3}$ – $\frac{1}{2}$ . **Corolla** 16–20 mm long, glabrous, apically straight, white; **stamens** 16–18 mm long.

Variety *albiflora* is found in disturbed areas of montane cloud forest and on remnant trees in pastureland, 950–1500 m elevation. It is endemic to the Cordillera de Tilarán of central Costa Rica. Flowering collections have been made in July–September; fruiting in September–November. **Endangered.**

Var. **coloradensis** Luteyn, Brittonia 28: 401. 1976.

**Inflorescence** rachis (2) 2.5–7 cm long, with or without scattered clavate glandular fimbriae; floral bract caducous or persistent, oblong to somewhat oblanceolate, 6–22 mm long, apex rounded or slightly notched, callose-apiculate; pedicels 10–19 mm long, with or without clavate glandular fimbriae; bracteoles broadly ovate to semi-orbicular, callose-apiculate. **Corolla** 29–32 mm long, glabrous or weakly pilose in apical  $\frac{1}{2}$ , rarely apically arcuate, blue; **stamens** 27–29 mm long.

Variety *coloradensis* is found in premontane to Continental Divide cloud forest, 1050–1750 m elevation. It is endemic to the Chiriquí highlands of Panama, where it has been collected at Cerro Colorado and in the vicinity of the Fortuna Dam site. Flowering collections have been made in all months from January through October; fruits unknown. **Locally Common.**

Var. **melastomoides**

**Inflorescence** rachis (3) 5–8 (15) cm long, usually scattered to densely glandular; floral bract caducous, oblong, oblanceolate, 6–14 (20.5) mm long, apex rounded or acute, never emarginate, pale green often with pinkish margins; pedicels (7) 10–21 (27) mm long, usually glandular as rachis; bracteoles narrowly ovate-lanceolate, glandular-callose in apical  $\frac{1}{3}$ – $\frac{1}{2}$ . **Corolla** (19) 26–37 (41) mm long, glabrous, apical portion often distinctly curved upward, dark reddish-maroon; **stamens** 19.5–34.5 mm long.

Variety *melastomoides* occurs in primary cloud forest, disturbed forest, remnant trees in pastureland, or fence-row trees, 1400–2800 m elevation.

It is endemic to the Cordillera Central and Cordillera de Talamanca, Costa Rica. Flowering collections have been made in April–July; fruiting in June–September. This variety is visited by the hummingbird *Lampornis calolaema* in Costa Rica (Luteyn, 1998). **Widespread.**

**Cavendishia osaensis** Luteyn & J. F. Morales, Brittonia 48: 514, fig. 1 A–D. 1996[1997]. Figure 12.

**Epiphytic shrubs**; mature stems subterete, bluntly angled, smooth or minutely striate, nitid, glabrous; twigs subterete, slightly angled, smooth, glabrous. **Leaves** with petioles rugose, 2–4 mm long, weakly short-pilose, glabrate; leaf blades coriaceous, ovate, lanceolate to ovate-elliptic, 7–11.5 cm long, 1.3–3.2 cm wide, base obtuse or rounded, apex gradually tapering and acuminate, glabrous, also with deciduous, minute, glandular fimbriae beneath, 3 (5)-plinerved, midrib impressed above, raised and conspicuous beneath, lateral nerves slightly raised but relatively inconspicuous above, slightly raised beneath, reticulate veinlets slightly raised and conspicuous above, slightly raised but obscure beneath. **Inflorescences** subspherical, congested, racemose, 4–11-flowered, surrounded at base by a series of ovate to oblong, glabrous bracts; rachis angled, 5–10 mm long, glabrous; floral bract smooth but venation conspicuous on both surfaces, obovate or oblong-elliptic, 16–24 mm long, base cuneate, apex obtuse or rounded, glabrous, pinkish-lilac; pedicels sometimes ribbed, 5.5–7 mm long, glabrous; bracteoles basal, ovate, ca. 1 mm long, marginally with thick cartilaginous teeth. **Flowers** with calyx 5–7 mm long, glabrous, tube cylindrical, slightly rugose, 1.5–2 mm long, base apophysate with a relatively smooth margin, limb spreading-campanulate, 3.5–5 mm long, lobes slightly striate, long-triangular, 2.5–3 mm long, erect after anthesis, margin scarious and bearing ca. 3–4 oblong to fimbriate glands basally, these becoming thickened cartilaginous teeth apically, sinuses obtuse; **corolla** cylindric, narrowed at throat, 1.8–2.2 cm long, 3–4.5 mm diam., basal  $\frac{2}{3}$  red and apical  $\frac{1}{3}$  white, lobes erect, somewhat ovate-triangular, 0.7–1 mm long, white; **stamens** overall equal, ca. 18 mm long; filaments alternately 2–3 mm and ca. 4 mm long, glabrous or weakly puberulent apically; anthers alternately ca. 17 mm and ca. 14.5 mm long, thecae ca. 4–5 mm long. **Berry** not seen.

*Cavendishia osaensis* is found in lowland rain forest, 200–750 m elevation. It is endemic to the Osa Peninsula of Costa Rica, where it is known from only the following five collections: Cantón de Golfito, Jiménez, Dos Brazos de Río Tigre, along trail toward the union of Quebrada Pate-mazo and Quebrada Porsillego (*G. Herrera 4636*) and at Cerro Rincón (*G. Herrera 4157*); Cantón de Osa, Reserva Forestal Golfo Dulce, Quebrada Vaquedano (*R. Aguilar & G. Herrera 806*), along the trail to Cerro Brujo, from Quebrada Vaque-

dano to the top (A. Fernández 161); and Rancho Quemado, Sierpe, around the lakes (J. Marín & F. Quesada 2612). Flowering specimens have been collected in January and November; fruits are unknown. **Endangered.**

*Cavendishia osaensis* is characterized by having a glabrous habit, gradually long-tapering and acuminate leaves, calyx lobes that are most of the length of the limb with glands that are broken up into ca. 3 or 4 oblong to spherical portions. Its relationships are not clear, although it belongs to *Cavendishia* ser. *Englerianae* and keys closest to *C. engleriana* var. *engleriana*.

***Cavendishia panamensis*** Luteyn, Brittonia 28: 47. 1976.

Erect, often arching, terrestrial **shrubs** 2.5–3 m tall; mature stems terete, glabrous, ca. 1 cm diam., the base ca. 2.5 cm diam.; twigs bluntly angled or ribbed, minutely striate, glabrous, often bearing tiny, sessile, blackish, spherical glands. **Leaves** with petioles slightly flattened adaxially, rugose, (2.5) 6–8 (10) mm long, 2–2.5 (3.5) mm diam., glabrous or infrequently puberulent; leaf blades elliptic, lance-elliptic to ovate-lanceolate, 9–16 cm long, 3–6 cm wide, base acute to narrowly obtuse, rarely rounded, apex acuminate to somewhat caudate acuminate, glabrous but often with caducous, scattered, reddish, pustular glands 0.1–0.2 mm diam. along upper surface that leave a reddish or blackish papillate scar, 5 (7)-plinerved, innermost lateral nerves often arising 2–3 cm above base, midrib impressed above, raised and conspicuous beneath, lateral nerves impressed above becoming plane to slightly elevated apically with outer lateral nerves often obscure beyond middle, raised and conspicuous beneath, veinlets raised and usually conspicuous above, obscure to slightly raised beneath. **Inflorescences** loosely cylindric, 11–21 (37)-flowered, viscid, often basal nodes sterile; rachis flattened, often flexuous apically, conspicuously ribbed and minutely striate, glabrous or rarely puberulent, (3) 8–17 cm long, to 5 mm diam. at base, pink to dark pink when fresh with minute, peltate, globular, reddish glands along length and especially at base; floral bract oblong to oblanceolate, rarely obovate, (2) 3–5 cm long, (0.6) 1–2 cm wide, narrowed to a slightly clasping base, apex rounded or narrowly obtuse to acute, pink, glabrous or sparsely ciliate along apical  $\frac{1}{2}$  of margin, marginally with 7–23 dark red, globular, peltate or sessile glands ca. 0.7 mm diam.; pedicels swollen apically, striate, (11) 15–19 mm long, 1–1.5 mm diam., pink, glabrous, with scattered, globular, reddish glands; bracteoles basal, ovate to lanceolate, 1.5–2 (4) mm long, 1–2 mm wide, pink with scattered, dark red, globular glands at apex and margins. **Flowers** with calyx glabrous, 4–6 mm long, tube cylindric or spreading, rugose to strongly ribbed, 1.5–2 mm long, ca. 2.5 mm diam., usually with dark red, globular to disc-shaped, peltate glands obscuring surface, limb cylindric-campanulate, (2.5) 3–3.5 mm long, with scattered, globular to disc-shaped, peltate glands, lobes triangular, obtuse, 1–1.5 mm long, ca. 1.5 mm wide, erect after anthesis, margin glandular callose thickened with glands

contiguous at lobe apices, sinuses concave; **corolla** cylindric, constricted at base, narrowed at throat, 2.5–3.5 cm long, 8–10 mm diam., glabrous or pilose but glabrous at constricted base, white, lobes triangular, obtuse, 1–2 mm long; **stamens** 27–30 mm long; filaments slightly coherent at base, strigose apically, alternately 4–6 mm and 10–13.5 mm long; anthers alternately 17–20.5 mm and 25–27 mm long, thecae 7.5–11 mm long. **Berry** not seen.

*Cavendishia panamensis* is endemic to cloud forest in western Chiriquí Province, Panama (Volcá Barú), 1830–1980 m elevation. It has not yet been found in Costa Rica. Flowering specimens have been collected in February, April, and May; fruits are unknown. **Endangered.**

*Cavendishia panamensis* is characterized by its glandular-margined floral bract and bracteoles and nonapophysate calyx tubes the surfaces of which are nearly covered by the globular glands. It belongs to *Cavendishia* ser. *Lactiviscidae*, where it differs from *C. chiriquiensis* by a basic difference in calyx lobe glands—in *C. panamensis* the callose-thickened portion of the calyx lobe is strictly marginal, while in *C. chiriquiensis* the entire calyx lobe is callose thickened and appears occasionally to break off.

***Cavendishia pseudostenophylla*** Luteyn, Brittonia 28: 46. 1976.

Terrestrial or epiphytic **shrubs**, sometimes lianoid; mature stems terete, minutely striate, puberulent; twigs subterete to bluntly angled, minutely striate, puberulent. **Leaves** with petioles subterete, rugose, 2–3.5 mm long, 1–2 mm diam., densely puberulent; leaf blades linear-lanceolate to linear-elliptic, strongly revolute, 9–14 cm long, 1–1.5 cm wide, base broadly obtuse or rounded, slightly cordate, apex long-attenuate, acute, glabrous, 3 (5)-plinerved, midrib deeply impressed above and raised and conspicuous beneath, lateral nerves and reticulate veinlets raised and conspicuous above and slightly raised but obscure beneath. **Inflorescences** loosely cylindric, viscid, 12–20-flowered, lowest nodes sterile; rachis long-tapering, bluntly angled, minutely striate, 5–15 cm long, ca. 1–1.5 mm diam., glabrous, bearing scattered globular glands; floral bract prominently veined, often somewhat ribbed, oblong or oval elliptic, (13) 19–27 mm long, (5) 7–11 mm wide, base narrowed and rounded, apex rounded or acute, apex short-ciliate, pink, margins bearing (3) 7–12 (per side) sessile, globular glands to 0.2 mm diam.; pedicels to 8 mm long, ca. 1 mm diam., glabrous, bearing few globular glands; bracteoles apical, completely enveloping flowers in bud, clasping calyx and corolla at anthesis, oblong, oblong-elliptic or oblanceolate, ca. 25 mm long, ca. 10 mm wide, base rounded, apex broadly rounded, glabrous but margin short-ciliate and bearing up to 15 globular glands. **Flowers** with calyx 6.5–7.5 mm long, glabrous, tube cylindric, slightly rugose, 1.5–2 mm long, ca. 3.5 mm diam., base slightly expanded and bearing globular

glands around margins and onto surface, limb campanulate or erect-spreading, smooth or slightly ribbed, 5–6 mm long, lobes triangular, ca. 2 mm long, margins conspicuously glandular callose-thickened, the thickenings nearly contiguous at apex of lobe, sinuses obtuse or rounded; **corolla** cylindric, ca. 32 mm long, ca. 6 mm diam., pink, densely short-pilose in apical  $\frac{1}{3}$ , lobes triangular, ca. 2 mm long; **stamens** 27–28 mm long; filaments alternately 4–4.5 mm and 7.5–8 mm long, short-pilose in apical  $\frac{1}{2}$ ; anthers alternately ca. 24–24.5 mm and 20 mm long, thecae 6–7 mm long. **Berry** not seen.

*Cavendishia pseudostenophylla* is known only from cloud forest in the Bocas del Toro/Chiriquí Province border area and tropical wet forest north of Santa Fé (Veraguas Prov.), Panama, 300–1100 m elevation. It has only been collected eight times in Panama and is not yet known from Costa Rica. Flowering specimens have been collected in April and May; fruits are unknown. **Endangered.**

*Cavendishia pseudostenophylla* is characterized by its leaves that are about nine times longer than wide, inflorescences and flowers with globular glands, prominently veined floral bracts, long and apical bracteoles that clasp the calyx and corolla at anthesis, a slightly apophysate calyx tube, and calyx lobes that are glandular callose-thickened. It is very reminiscent of *C. stenophylla* A. C. Smith (Coclé and Panamá Prov., Panama). Closer examination of the leaves of *C. pseudostenophylla*, however, shows them to be plinerved and apically acute, in contrast to the obscurely pinnately nerved and apically obtuse leaves of *C. stenophylla*. Other characters, especially differences in bracteole size and position, also distinguish the two species.

**Cavendishia pubescens** (Kunth in H.B.K.) Hemsl., Biol. Cent.-amer., Bot. 2: 273. 1881. *Thibaudia pubescens* Kunth in H.B.K., Nov. Gen. Sp. 3: 273. 1819. *Proclesia pubescens* (Kunth in H.B.K.) Klotzsch, Linnaea 24: 33. 1851. *Chupalon pubescens* (Kunth in H.B.K.) Kuntze, Rev. Gen. Pl. 2: 383. 1891.

Epiphytic and terrestrial **shrubs** 1–3 m tall; mature stems subterete or bluntly angled, ridged, moderately short-pilose to glabrate; twigs flattened and coarsely angled, ridged, densely short-pilose with whitish or grayish trichomes ca. 0.5 mm long. **Leaves** with petioles terete to often adaxially flattened, rugose, sometimes coarsely ridged, (6) 9–15 mm long, 2–3.5 mm in diam., densely short-pilose or puberulent; leaf blades elliptic, oblong-elliptic, lanceolate or ovate, (5.5) 14–20 (30) cm long, (1.5) 3.5–9 (12.5) cm wide, base cuneate, obtuse, rounded, cordate or truncate, apex long-acuminate with a blunt or sharply acute tip, usually densely puberulent to short-pilose on both surfaces with soft, white trichomes, per-

sistent beneath but often glabrate above, 5–7-plinerved, midrib impressed above and prominently raised beneath, lateral nerves impressed above but plane apically, raised and prominent beneath, veinlets plane to slightly raised or conspicuously impressed above but obscure beneath. **Inflorescences** capitate to obovate, 7–11-flowered, encircled at base by densely matted or appressed short-pilose bracts; rachis bluntly angled, striate, rugose, persistently densely short, white pilose, sometimes with glandular fimbriae, 1–2.5 (4.5) cm long and 2–3 mm in diam., rarely with cartilaginous teeth at base; floral bract muricate, elliptic to oblanceolate, 17–30 mm long, 7–13 (17) mm wide, base narrowed, apex rounded or rarely emarginate, pale pinkish-green or whitish-green through dark pink to red, often with small, red, clavate glands abaxially, glabrous or only ciliate, to sparsely or densely short, white and usually appressed pilose both abaxially and marginally, sometimes fimbriate along margin; pedicels bluntly angled, densely short-pilose, often fimbriate, 6–14 mm long and 1–1.5 mm in diam.; bracteoles oblong, linear, or subulate, 2–4.5 (5) mm long, ca. 1 mm wide, densely pubescent or only marginally ciliate, margin glandular-fimbriate, the fimbriae rarely fusing apically. **Flowers** with calyx (4.5) 5.5–8 mm long, pubescent with densely matted, white or tan trichomes, glandular-fimbriate, tube cylindric, usually shorter than limb, (2) 2.5–4 mm long, limb campanulate or spreading, (2.5) 3–5 mm long, lobes oblong, oblong-triangular, broadly triangular or deltoid, (1) 1.5–3 mm long, 1.5–1.7 mm wide, apex obtuse or broadly rounded, sometimes then apiculate, connivent or curling after anthesis, rarely reflexed, marginally glandular-fimbriate, the fimbriae rarely fusing apically, sinuses obtuse; **corolla** cylindric or bottle-shaped, slightly constricted at base, narrowed at throat, (12) 15–20 (22) mm long, 7–8 mm in diam., white or tinted pink, with age becoming red, moderately to densely short-pilose with white or tawny trichomes, lobes triangular, ca. 1–2 mm long, wide-spreading at anthesis; **stamens** 10–15.5 mm long; filaments alternately (1.8) 2.5–4 mm and 3.5–6 mm long; anthers alternately 9.5–13 mm and 8–11 mm long, thecae 2.5–4 mm long. **Berry** spherical, densely puberulent, 8–14 mm in diam., dark maroon to blue-black.

*Cavendishia pubescens* is found in relatively dry exposed slopes and thickets, although a few labels indicate its presence in humid or rain forest, (700) 1200–2100 (3000) m elevation, in western Panama (within 20 km of the border with Costa Rica), and from Venezuela to Bolivia. It has not yet been found in Costa Rica. Flowering and fruiting occur throughout the year. **Rare/Infrequent** (in Panama).

*Cavendishia pubescens* is readily distinguished by its pale pinkish to rose or whitish-green floral bracts, densely short-pilose, white to pinkish-white corollas, densely pilose to matted or woolly calyces of which the limb is longer than the tube and the lobes are oblong and obtuse, and persistently soft-puberulent or pilose leaf undersurfaces and fruits. The densely matted pubescence of the

calyx is usually enough to characterize the species. *Cavendishia pubescens* belongs to ser. *Cavendishiae*, where it is most closely related to *C. bracteata* (see that species). *Cavendishia pubescens* may hybridize with *C. bracteata* (Luteyn, 1976c). The species is visited by hummingbirds (pers. observ.).

***Cavendishia quercina*** A. C. Smith, Contrib. U.S. Natl. Herb. 28: 450. 1932. Illustration: J. L. Luteyn, Mem. New York Bot. Gard. 28(3): 109, fig. 56. 1976. Figure 6.

Terrestrial or epiphytic **shrubs** 0.5–2 m tall; mature stems densely puberulent, glabrate. **Leaves** with petioles (1) 2–4 (6) mm long, densely short-puberulent, often glabrate; leaf blades oblong, oblong-ovate or ovate, 2.5–7.5 cm long, (1) 1.5–3.5 cm wide, base rounded and subcordate, clasping, apex rounded, obtuse or often subacute, usually densely short-pilose on both surfaces but persistent only on the upper surface, 3–5 (7)-plinerved. **Inflorescences** loosely cylindric, 12–20 (53)-flowered; rachis 2–12 cm long, glabrous or densely hirsute; floral bract oblong or oblong elliptic, (9.5) 11–18 (23) mm long, base rounded to obtuse, not clasping, apex obtuse or rounded, glabrous or margin short-ciliate, margin glandular fimbriate, red; pedicels (6.5) 10–14 (18) mm long, sparsely to densely hirsute or rarely glabrate, dark pink but turning greenish; bracteoles oblong or oblong-ovate, 1–3 (5.5) mm long, glabrous, ciliate, or short-pilose at apex, margin densely glandular-fimbriate. **Flowers** with calyx (5.5) 6–8 (9) mm long, sparsely to densely hirsute or rarely glabrous, red, tube short-cylindric, often 5-ribbed, rugose, 1.5–2.5 (3) mm long, basally apophysate, limb cylindric, spreading-erect or rarely campanulate, smooth, rugose or sometimes ribbed, (3.5) 4–6 (6.5) mm long, lobes 1–2.5 mm long, narrowly or sometimes broadly triangular, erect after anthesis, marginally short-ciliate and provided along each side with 3–5, intermittent, stout, glandular-thickenings that may coalesce, sinuses concave, usually ciliate; **corolla** cylindric, slightly constricted at base, (8.5) 11.5–15 (17.5) mm long, 2.5–4.5 mm diam., densely pilose apically, rarely glabrous, pale pinkish at base becoming pale green above, lobes whitish to pinkish-green, lobes ca. 2 mm long, oblong; **stamens** 8–15 mm long; filaments alternately 2–5 mm and 3–8 mm long, pilose apically; anthers alternately 5–9.5 mm and 6.5–12 mm long, thecae 1–4 mm long. **Berry** spherical, at least 8–9 mm diam., weakly pilose, dark blue-black.

*Cavendishia quercina* is infrequently found in cloud forest, 1050–2300 m elevation. It is distributed from the eastern Cordillera de Tilarán of Costa Rica east through the Central Valley and Cordillera de Talamanca to western Chiriquí Province (Volcán Barú), Panama. Flowering occurs throughout the year but is most abundant from October to March; fruiting specimens have been

collected in January, February, and April through June. **Widespread.**

*Cavendishia quercina* is characterized by its short, oblong-ovate leaf blades with subcordate bases and rounded or subacute apices, hirsute rachises, pedicels and calyces, short-pilose to almost woolly corollas, stout calyx lobe glands, and densely glandular-fimbriate bracteoles. It is easily recognized in the field by the leaves, the deep red floral bracts and calyces, and the pale green corollas with whitish tips. It belongs to *C. ser. Cavendishiae*, where it is most similar to *C. ruiz-teranii* Luteyn from Venezuela. It is also similar to *C. capitulata*, in which occasionally the glandular fimbriae of the calyx lobes seem to fuse to form the stout, more or less oblong glands and by similar extremes in leaf variation. A comparison of the important characters of *C. quercina*, along with other Costa Rican members of sect. *Quereme*, is given in Table 1.

***Cavendishia quereme*** (Kunth in H.B.K.) Benth. & Hook.f., Gen. Pl. 2: 570. 1876. *Thibaudia quereme* Kunth in H.B.K., Nov. Gen. Sp. 3: 274, table 256. 1819. *Polyboea quereme* (Kunth in H.B.K.) Klotzsch, Linnaea 24: 31. 1851. *Chupalon quereme* (Kunth in H.B.K.) Kuntze, Rev. Gen. Pl. 2: 384. 1891. Illustration: J. L. Luteyn, Mem. New York Bot. Gard. 28(3): 104, fig. 51. 1976. J. L. Luteyn, Fl. Neotrop. Monogr. 35: 247, fig. 74D–F. 1983. Figures 9 and 14.

Terrestrial or epiphytic **shrubs** 1–2.5 m tall; mature stems glabrous and with odor of wintergreen. **Leaves** with petioles terete or subterete, (3) 5–7 (9) mm long, glabrous at maturity; leaf blades bullate, elliptic, lance-elliptic or lanceolate, rarely ovate, (3.5) 6–11 (14) cm long, (1) 1.5–4 (5) cm wide, base acute or obtuse or rounded and short-attenuate, usually somewhat short-decurrent on petiole, apex acuminate or caudate-acuminate, glabrous, 5 (7)-plinerved. **Inflorescences** loosely cylindric, (8) 12–20 (25)-flowered; rachis 2–5 (6) cm long, glabrous; floral bract conduplicate and slightly keeled, ascending, oblong, elliptic or lanceolate, 10–25 mm long, base rounded to obtuse, slightly clasping, apex acute, margin glandular-fimbriate, glabrous, pink or red; pedicels (5) 8–16 (19) mm long, glabrous, pinkish-green; bracteoles basal, lanceolate, oblong or linear-lanceolate, rarely ovate, 1–2.5 (5) mm long, 0.5–1 (2) mm wide, apex acute or obtuse, margin glandular-fimbriate. **Flowers** with calyx 2.5–5 mm long, glabrous, tube basically cylindric but pentagonal with broad, blunt angles, smooth or rugose, 1.5–2 mm long, limb cylindric, slightly spreading or campanulate, 2–3.5 mm long, lobes 1–1.5 mm long, ovate or oblong, acute to bluntly apiculate, connivent after anthesis, marginally thin lacerate-glandular, sinuses acute; **corolla** bottle-shaped, pentagonal,

7–11 (13) mm long, 3–6 (7) mm diam., glabrous, whitish at constricted base, then becoming orange or reddish-orange through the middle half and then white at throat, lobes ca. 1 mm long, white; **stamens** alternately 5.5–7.5 mm and 8–9.5 mm long; filaments alternately 1.5–2 (3.5) mm and (2.5) 3.5–5 mm long; anthers alternately (4.5) 5.5–7.5 mm and (3.5) 5–6.5 mm long, thecae 1.5–3 mm long. **Berry** spherical, 7–11 mm diam., blue-black.

*Cavendishia quereme* is found as an epiphyte in rain forest and montane cloud forest and as a terrestrial shrub in disturbed areas along trails or roadsides, 600–1700 m elevation. It has a disjunct distribution from the Central Valley (Alajuela Prov.) of Costa Rica to western Panama (Chiriquí Prov.) and then again in the Cordillera Occidental (Valle and Nariño Depts.) of Colombia. Flowering and fruiting occur sporadically throughout the year. **Locally Common.**

*Cavendishia quereme* is a very pretty species characterized by nitid, coriaceous, bullate leaf blades; dark pink floral bracts; a bottle-shaped corolla that is bluntly pentagonal and bright orange with white lobes; and stamens that are conspicuously alternately unequal to each other in length. One of its most distinctive characters is the very strong odor of wintergreen (methyl-salicylate), which is emitted by the vegetative parts of the plant (Luteyn, 1976c; Luteyn et al., 1980). The odor is so distinctive that it can often be smelled in the field before it is seen, and it persists in the herbarium even after the plants have been dried by heat whether pretreated with formaldehyde or ethanol or preserved in FAA. *Cavendishia quereme* is morphologically remarkably uniform despite its disjunct distribution. There is so little interpopulational variation that specimens from Colombia, Costa Rica, and Panama are indistinguishable. *Cavendishia quereme* belongs to *C.* sect. *Quereme*, where it is presumably most closely related to *C. laurifolia* (Klotzsch) Benth. & Hook.f. from Guatemala, Panama, and adjacent Colombia, both taxa having similar habits, pronounced bottle-shaped and bluntly pentagonal corollas, lacerate-glandular calyx lobes, and stamens that are conspicuously alternately unequal in overall length. *Cavendishia quereme* differs from *C. laurifolia* by its bullate and glabrous leaf blades (not flat and puberulous); the absence of glandular fimbriae from corollas, calyces, and pedicels; conuplicate-keeled and ascending floral bracts (not concave and perpendicular to recurved from rachis); shorter pedicels (8–16 mm vs. 14–22 mm long); and corolla color (orange with white vs. red

with white). A comparison of the important characters of *C. quereme*, along with other Costa Rican members of sect. *Quereme*, is given in Table 1. *Cavendishia quereme* putatively hybridizes with *C. endresii* and *C. axillaris* in Costa Rica and western Panama (Luteyn, 1976c). A common name in Costa Rica (San José Prov.) is *colmillo*. This species is visited by hummingbirds (pers. observ.).

***Cavendishia subfasciculata*** Luteyn, Brittonia 28: 50. 1976.

Terrestrial or epiphytic **shrubs** 0.7–3 m tall, sometimes lianoid; mature stems terete, smooth or minutely striate, glabrous, usually with a thin, whitish waxy layer; twigs subterete to bluntly angled, striate, often coarsely ridged, glabrous. **Leaves** with petioles usually flattened adaxially, rugose and often coarsely ridged, 7–13 mm long, 1.5–2 mm diam., glabrous to weakly pilose adaxially when young, often glabrate; leaf blades coriaceous, lanceolate to lance-elliptic, (3) 5–9 (11) cm long, (1) 2–4 cm wide, base obtuse or rounded, often short-decurrent onto petiole, apex often abruptly short-acuminate, glabrous or often with numerous, short trichomes at base of midrib adaxially, usually glabrate, 5 (7)-plinerved, midrib plane or more commonly weakly impressed above, lateral nerves usually raised and conspicuous or rarely weakly impressed above and raised beneath, reticulate veinlets raised and conspicuous to obscure above and obscure beneath. **Inflorescences** obconic to spherical in bud, (2) 3–6 (9)-flowered; rachis flattened, bluntly angled, striate, viscid, (0.3) 0.6–1.2 (3.2) cm long, glabrous, usually bearing minute, cartilaginous teeth basally; floral bract smooth or rarely slightly ribbed, oblong to oblanceolate or oblong-lanceolate, (1.5) 2–3 (4) cm long, 0.5–1 (2) cm wide, base narrowed and somewhat auriculate, apex rounded or obtuse and usually emarginate or when young with the notch almost completely filled with callose tissue, glabrous, usually bearing minute, red, glandular fimbriae abaxially, pale green but suffused with pink along margins and basally, usually translucent; pedicels swollen apically, ridged, (6) 8–13 (–15) mm long, (0.5) 1–1.5 mm diam., glabrous, occasionally with cartilaginous teeth at apical tip; bracteoles linear-lanceolate, 1–2.5 (3) mm long, 0.5–1 mm wide, apex acuminate and glandular callose-thickened in apical  $\frac{1}{2}$ – $\frac{2}{3}$ . **Flowers** with calyx 5–7 (10) mm long, glabrous, tube cylindric, weakly rugose, strongly ribbed, (1.5) 2–3 (4) mm long, basally apophysate and deeply lobed with these lobes straight and extending to or just beyond articulation, limb campanulate to cylindric, smooth or weakly ribbed and minutely papillate, (2.5) 3.5–4.5 (6) mm long, lobes triangular, (0.7) 1–1.5 (2) mm long, 2–3 mm wide, sometimes flaring but later erect, glandular callose thickened throughout or only in apical  $\frac{2}{3}$ , sinuses obtuse, concave or flat; **corolla** thinly carnose, cylindric, slightly constricted at base and narrowed to throat, often translucent, 20–24 (30) mm long, 5–7 mm diam., glabrous or rarely pilose, whitish at base and apex but otherwise pinkish-violet to rose-red, lobes triangular or oblong, ca. 1 mm long, reflexed, apex acute and often callose thickened, white with pinkish or violet



margins; **stamens** 19–24.5 mm long; filaments alternately 2.5–5 mm and 5–10 mm long, densely pilose; anthers alternately 13–20 mm and 17–22 mm long, thecae 4.5–7 mm long. **Berry** ca. 9 mm diam., blue-black.

*Cavendishia subfasciculata* is endemic to western (Chiriquí Prov.) and central (Veraguas Prov.) Panama, where it is found in premontane and montane cloud forest, 1100–2600 m elevation. It has not yet been found in Costa Rica. Flowering specimens have been collected from December to August; immature fruits in March. **Rare/Infrequent.**

*Cavendishia subfasciculata* is characterized by having capitate, few-flowered inflorescences, emarginate and translucent floral bracts, apophysate and deeply lobed calyx tubes, glandular-callose calyx lobes, and relatively short corollas with callose-thickened lobes. It has two slightly different color phases that are correlated with geography. In western Chiriquí Province (Panama), around Boquete, the floral bracts are greenish to pinkish-green and the corollas pinkish-violet to rose-red, while in eastern Chiriquí Province, around the Fortuna Dam site, and in Veraguas Province, the bracts are pink and the corollas pink to white. Within sect. *Callista*, *C. subfasciculata* is likely most closely related to *C. morii* Luteyn and its allies, all normally having glandular-callose corolla lobes. However, it also shows morphological similarities to *C. megabracteata*, based on emarginate floral bracts; few-flowered, obconoid to spherical inflorescences; similarly colored floral bracts and corollas; and glandular-callose corolla lobes. *Cavendishia subfasciculata* may be distinguished from *C. megabracteata* by its overall smaller size, its fuller and more dense habit, its usually green floral bracts (pinkish or pale purple bracts of *C. megabracteata*), slightly decurrent leaf bases, and leaf venation.

**Cavendishia talamancensis** Luteyn, Brittonia 28: 43. 1976. Illustration: J. L. Luteyn, Mem. New York Bot. Gard. 28(3): 102, fig. 49. 1976. Figure 6.

Terrestrial or epiphytic **shrubs** 0.5–2 m tall; mature stems glabrous; twigs densely short-pilose, all pubescence curly. **Leaves** with petioles 3–4 (6) mm long, densely puberulent; leaf blades bullate, oblong or oblong-ovate, (2) 3.5–5.5 (7) cm long, (1.5) 2–4 (4.5) cm wide, base rounded and subcordate, apex rounded or obtuse, densely short-pilose along nerves and margins when young, 3–5 (7)-plinerved. **Inflorescences** short-cylindric, compact, 8–32-flowered; rachis 1–9 cm long, densely crisped, short-pilose; floral bract ribbed, oblong

or oblong-elliptic, 8–10 mm long, base rounded, somewhat clasping rachis, apex rounded and often shallowly emarginate, glabrous or densely short-pubescent, margin ciliate and glandular-fimbriate, purplish; pedicels (1.5) 4.5–7 mm long, densely short-pilose, rarely glabrate, usually with tiny, black, clavate glands apically; bracteoles basal, ovate or subulate, (0.5) 1–2 mm long, usually densely short-pilose and also densely glandular-fimbriate marginally. **Flowers** with calyx 6–9 mm long, usually densely short-pilose, rarely glabrate, tube barrel-shaped, strongly rugose, 2–3 (3.5) mm long, basally short-apophysate, limb cylindric or somewhat spreading, rugose, 3.5–6 mm long, lobes 1.5–2 mm long, oblong-ovate or ovate, usually somewhat connivent after anthesis, margin lacerate-glandular, sinuses acute; **corolla** cylindric, 11.5–14 mm long, 4–5 mm diam., pilose apically, rarely glabrate, pink, pinkish-white or purplish, lobes oblong-deltate to triangular, acute, ca. 1–1.3 mm long; **stamens** 8.5–10.5 mm long; filaments alternately 2.5–3.5 mm and 3.5–5.5 mm long, pilose apically; anthers alternately 6.5–8.5 mm and 5–7.5 mm long, thecae 1–3 mm long. **Berry** not seen.

*Cavendishia talamancensis* is found in montane, *Quercus* cloud forest, wet thickets, and steep rocky road cuts, 2000–3000 m elevation. It is a rare species, endemic to the Cordillera de Talamanca (Cartago and San José Provs.) in Costa Rica. Flowering specimens have been collected in December–February and April–August; immature fruiting specimens only in January. **Rare/Infrequent.**

*Cavendishia talamancensis* is characterized by leaf blades that are small, bullate, oblong, or oblong-ovate, basally subcordate and apically rounded or obtuse; densely crisped-pilose inflorescences (rachis, floral bracts, pedicels, and calyces); and lacerate-glandular calyx lobes. Its morphological features are compared with other members of *Cavendishia* sect. *Quereme* in Table 1. Although without close relatives, it is vegetatively similar to *C. quercina* but differs by the characters of calyx lobe glands and tube. Occasional populations of *C. talamancensis* are reported to emit the odor of wintergreen from crushed leaves, which may indicate a relationship with *C. quereme*.

**Cavendishia wercklei** Hoerold, Bot. Jahrb. Syst. 42: 325. 1909. Illustration: J. L. Luteyn, Mem. New York Bot. Gard. 28(3): 119, fig. 66. 1976.

Terrestrial or epiphytic **shrubs** to 2 m tall; mature stems usually glabrous but sometimes scattered spreading hirsute; twigs frequently with reddish, clavate glands. **Leaves** with petioles (5) 6–11 (12) mm long, densely short-pilose, occasionally glabrous; leaf blades lanceolate, lance-elliptic, oblong or rarely ovate, (4) 7–12 (15) cm long, (1) 2–4 (5) cm wide, base rounded, cuneate or obtuse, apex long-acuminate, weakly pilose

along nerves and lamina base and then glabrate, or pubescence persisting along nerves on adaxial surface, 3–5-plinerved. **Inflorescences** loosely cylindric, (6) 9–12 (19)-flowered; rachis (3) 5–7 (9) cm long, 2–4 mm diam. at base, glabrous, viscid, densely covered by sessile to subsessile, globular or clavate, reddish glands ca. 0.2 mm long; floral bract oblong to obovate, (15) 20–30 (35) mm long, apex obtuse to rounded and rarely apiculate, usually caducous, usually conspicuously nerved, glabrous, rose to pinkish-purple, abaxially with minute subsessile clavate reddish glands; pedicels (9) 11–18 mm long, viscid, glabrous, usually with reddish, sessile glands over entire length or only at base, rarely eglandular; bracteoles ovate or oblong-lanceolate, 2–4.5 (5) mm long, apex acute and glandular-thickened, usually conspicuously 3–5-nerved. **Flowers** with calyx 6–9 (11) mm long, glabrous, viscid, tube cylindric, coarsely ribbed, 2–3.5 (5) mm long, basally apophysate with margin undulate, limb cylindric to campanulate, smooth to ribbed, rarely minutely papillate, (3.5) 4–6 (6.5) mm long, lobes 1.5–2 mm long, triangular, obtuse or acute, erect after anthesis, completely glandular-thickened and this extending onto limb surface, sinuses obtuse, concave or rarely flat; **corolla** cylindric, narrowed at base, slightly constricted at throat, (25) 31–38 mm long, 6–8 mm diam., viscid, short-pilose for apical  $\frac{2}{3}$  or sometimes velutinous, whitish to purplish-rose, lobes 1.5–2 mm long, oblong, obtuse; **stamens** 26–34 mm long; filaments alternately 3.5–5.5 mm and 8–11.5 mm long, pilose apically; anthers alternately 25.5–31 mm and 20.5–24 mm long, thecae 5.5–10.5 mm long. **Berry** spherical, when immature at least 15 mm diam. and dark maroon.

*Cavendishia wercklei* is found in premontane forest, 1000–1500 m elevation. It is a rare species, endemic to the Central Valley of Costa Rica, having been collected mostly at La Palma de San José and in the vicinity of Vara Blanca (Alajuela Prov.); it is known from fewer than 10 collections. Flowering specimens have been collected in May and June. **Endangered.**

*Cavendishia wercklei* is characterized by its stout rachis; large, usually caducous floral bracts; glandular-fimbriate rachis and pedicels; 3–5-nerved bracteoles; undulate apophysis base; and whitish to pinkish-rose, apically short-pilose corollas. Within *C. sect. Callista*, it is related to *C. melastomoides* and *C. callista* and is distinguished by the characters mentioned above, as well as color, particularly that of the corollas and floral bracts. *Cavendishia wercklei* apparently hybridizes with *C. endresii* (Luteyn, 1976c). The species is visited by hummingbirds (pers. observ.).

## Chimaphila Pursh

REFERENCE—L. J. DORT, *Chimaphila*. Fl. Neotrop. Monogr. 66: 37–46. 1995.

**Herbs** or **subshrubs**, erect (rarely decumbent), the mature stems simple or branched at the base. **Leaves** alternate to subopposite, clustered in pseudo-whorls along stem, petiolate, the blade coriaceous, margin serrate, the venation pinnate. **Inflorescences** terminal, a pedunculate corymb or subumbel, or rarely flowers solitary; peduncles naked but subtended by persistent bud scales of winter bud from which it emerges; pedicels subtended by deciduous or persistent (then adnate) bracts, slightly recurved in flower, erect in fruit; bracteoles lacking. **Flowers** 5-merous, actinomorphic, fragrant; calyx persistent, with sepals distinct or shortly connate at base, lobes imbricate at base; **corolla** crateriform, aestivation imbricate, the petals distinct, spreading to reflexed, margin fimbriolate; **stamens** 10, equal, distinct, lacking appendages; filaments dilated at or below middle; connectives lacking disintegration tissue or spurs; anthers with thecae smooth, tubules short,  $\pm$  spreading, dehiscing by obliquely and slightly introrse pores; pollen in tetrads; ovary superior, 5-locular, depressed-globose, subtended by a 5-lobed, nectariferous disc; style massive, subsessile, fleshy, obconical or turbinate, embedded in summit of ovary; stigma broad, pelate, rounded, entire or with 5 undulate lobes. **Fruit** an erect, loculicidal capsule, dehiscence starting from both above and below, proceeding toward middle, the sutures smooth, lacking connecting threads; seeds numerous, small, winged; embryos undifferentiated, without developed cotyledons.

The genus *Chimaphila* consists of five species distributed in Eurasia, the West Indies, and North America south to Panama. One species occurs in Costa Rica. *Chimaphila* is distinct from all other Costa Rican Ericaceae, being characterized by its herb-like habit, leaves in pseudo-whorls, broadly crateriform corollas with distinct petals, staminal filaments conspicuously dilated, and superior ovary.

**Chimaphila maculata** (L.) Pursh, Fl. Amer. Sept. 1: 300. 1814. *Pyrola maculata* L., Sp. Pl. 396. 1753. *C. costaricens* Andres, Verh. Bot. Vereins Prov. Brandenburg 56: 66. 1914 (nom. nud.). *C. guatemalensis* Rydberg, N. Amer. Fl. 29(1): 32. 1914. Figures 1B and 15.

Herb-like, suffrutescent **subshrubs** 10–53 cm tall. **Leaves** spreading, clustered in 2–5 pseudo-whorls of 3–5 leaves each along stem, the pseudo-whorls separated by 1–7 cm long internodes, with petioles 3–13 mm long; leaf blades thick-coriaceous, lanceolate, oblong-lanceolate, ovate-lanceolate or ovate, 2–10 cm long, 0.8–3 cm wide, base obtuse, rounded or widely cuneate, apex acute or acuminate, margin sharply and remotely serrate, almost spine-tipped, dark green above and marked with a broad, whitish line along midrib and larger secondary veins, pale reddish-purple below. **Inflorescences** (1) 2–5-flowered; peduncles 7–11 cm long, finely papillate; pedicels 20–30 mm long, finely papillate; floral bract linear to linear-lanceolate, 2–4 mm long, apex acute, the margin dark brown, papillate near base, slightly dentic-



ulate. **Flowers** nodding to divergent; calyx 3–6 mm long, lobes ovate, 2–5 mm long, apex obtuse to rounded, margin finely dentate, ciliate, reflexed in fruit; **corolla** broadly crateriform, petals obovoid to orbicular, narrowing at base, 8–9 mm long, ca. 6 mm wide, margin ciliate, waxy white to pinkish; **stamens** 6–8 mm long; filaments ca. 4 mm long, the dilated portion villous with broad, flat, translucent hairs; anthers 2.5–3.5 mm long, pink, thecae 1.5–2 mm long, tubules 1–1.5 mm long. **Capsule** erect, depressed-spherical, 5–10 mm long and in diam., green turning black.

*Chimaphila maculata* is found on the forest floor in montane (including *Quercus*) forest, 2000–3000 m elevation. It is distributed from eastern North America south through Mexico to western Panama (Bocas del Toro Prov.). In Costa Rica and adjacent western Panama, it is known from only six collections from both slopes of the Cordillera de Talamanca. Flowering specimens have only been collected in March, April, July, and August; fruiting in August, September, and December–January. **Rare/Infrequent.**

*Chimaphila maculata* is characterized by leaves that are lustrous or shiny dark green above with a broad, whitish line along the midrib and larger secondary nerves and pale reddish-purple beneath and coarsely serrate margins. Throughout its extensive range, there is much variation in leaf morphology and degree of maculation, with numerous populations, especially in Mexico, being formally recognized (Rydberg, 1914; Camp 1939; Dorr, 1995). One variable species is herein recognized. *Chimaphila maculata* is probably most closely related to *C. umbellata* (L.) W. P. C. Barton, another species of widespread temperate and boreal distribution but with isolated populations in the mountains of Mexico, Guatemala, and on the island of Hispaniola. The two species differ most conspicuously in that *C. maculata* has maculated leaf blades that are coarsely serrate the entire length (vs. green leaf blades that are finely serrate, often only in the apical margins in *C. umbellata*) and villous staminal filaments (vs. glabrous or papillate).

## Comarostaphylis Zuccarini

REFERENCE—G. M. Diggs, *Comarostaphylis*. Fl. Neotrop. Monogr. 66: 146–193. 1995.

Erect to spreading, rarely trailing **shrubs** to small trees; bark exfoliating. **Leaves** alternate, petiolate, the blade bifacial, usually coriaceous, margin entire or

toothed, the venation pinnate. **Inflorescences** usually terminal, paniculate (in ours); pedicels continuous with calyx; bracteoles 2, basal to apical. **Flowers** (4) 5-merous, apparently without odor; calyx synsepalous, persistent in fruit, lobes much longer than tube, separate or slightly imbricate at anthesis, appressed to corolla, spreading to reflexed in fruit; **corolla** sympetalous, aestivation imbricate, cylindric to nearly globose, glabrous or pubescent, lobes much shorter than tube; **stamens** (Fig. 1D) 10, equal; filaments dilated near base; connectives with disintegration tissue present, with 2, abaxial, recurved, horn-like spurs; anthers ovoid, the surface smooth, dehiscing by 2, introrse pores/slits  $\frac{1}{4}$ – $\frac{1}{3}$  to nearly  $\frac{1}{2}$  as long as anther; pollen grains in tetrahedral tetrads, lacking viscin threads; ovary superior, papillate; ovule 1 per locule. **Fruit** drupaceous, globose, juicy, the surface warty, granular or papillate, the nutlets united into a solid, spheroidal, thick-walled, stone-like endocarp; seed 1 per nutlet, 1–1.5 mm long.

*Comarostaphylis* consists of 10 species distributed in the United States (especially southern California), south through Mexico to western Panama (Chiriquí Prov.). It is characterized by its superior ovary and drupaceous, warty fruit. One species occurs in Costa Rica.

**Comarostaphylis arbutoides** Lindl., Edward's Bot. Reg. 29: 30. 1843. *Arctostaphylos arbutoides* (Lindl.) Hemsl., Biol., Cent.-amer., Bot. 2: 278. 1881. Figure 10.

Erect to spreading, much-branched, evergreen **shrubs** to small trees 1–20 m tall; bark gray, tan, reddish-brown or brown; twigs glabrous and sometimes glaucous or glandular hirsute to ferruginously tomentose, the trichomes glandular or eglandular. **Leaves** with petioles 4–20 mm long, glabrous and sometimes glaucous or with indumentum as twigs; leaf blades lanceolate to elliptic, ovate or obovate, 4.5–12.5 cm long, 1–4.5 cm wide, base cuneate, apex obtuse to acute, margin sometimes undulate or with a few serrations, upper surface glabrous or scattered pilose, lower surface glabrous or with ferruginous eglandular tomentum to nearly woolly, midrib glabrous or with glandular or eglandular hairs marginally plane or revolute, rarely with a few serrations. **Inflorescences** terminal, densely paniculate, 3.5–13.5 (18) cm long, the rachis, pedicels, bracts, bracteoles and calyx glabrous or tomentose to glandular hirsute; floral bract lanceolate, nearly plane to navicular or carinate, 2.5–10 mm long, apex acuminate, ciliate or not; pedicels 5–8 mm long; bracteoles basal to nearly apical, 1.5–4 mm long, ciliate or not. **Flowers** with calyx lobes 1.7–2.5 mm long, 1.4–2 mm wide, triangular to ovate, acute to acuminate, glabrous or pubescent, trichomes glandular or not, often ciliate, strongly reflexed in fruit; **corolla** membranous, unistratose, broadly urceolate, 5.7–8 mm long, 4–6 mm diam., glabrous or pubescent, greenish-white to cream, pale yellow or white, sometimes suffused with pink, lobes 1–1.7 mm long, the margins often bluntly erose; **stamens** 2.5–3.2 mm long; filaments 2.4–3 mm long, villous; anthers 1–1.5 mm long, the spurs

0.4–1 mm long. **Drupe** ovoid to globose, 4–6 (7) mm diam., conspicuously warty, glabrous.

*Comarostaphylis arbutoides* ranges from Mexico (Chiapas) to western Panama. It is found in montane *Quercus* forests, cloud forests, and páramo, 1350–3800 m elevation, in the understory and as an important species in succession. This species “forms arbutoid ectomycorrhizal associations with members of the Agaricales, Boletales, and Russulales. The roots of the plant take on a definitive morphology and anatomy. Above timberline, in the páramo zone of the Talamancas, the plant can form extensive thickets, or in some sites,

semi-open mono-dominant stands occur” (Halling, pers. comm. and <http://www.nybg.org/bsci/res/hall/arbutoides.html>).

*Comarostaphylis arbutoides* is distinguished from its congeners by its large and entire leaf blades, densely panicle inflorescences, and southern distribution. It is morphologically most similar to *C. discolor* (Hooker) Diggs, from which it is separated by minor leaf blade differences (shape, serrations) and slightly denser inflorescences; *C. discolor* also grows several hundred kilometers to the north (Diggs, 1995). It has two subspecies that are distinguished by the following key:

**Key to the Subspecies of *Comarostaphylis arbutoides***

- 1a. Leaf blades ferruginous tomentose beneath; twigs, petioles, and calyx lobes pubescent; Cordillera de Talamanca to W Panama ..... subsp. *arbutoides*
- 1b. Leaf blades glabrous beneath; twigs, petioles and calyx lobes glabrous; central volcanic highlands of Costa Rica ..... subsp. *costaricensis*

Subsp. **arbutoides**. *Comarostaphylis chiriquensis* Camp, Ann. Missouri Bot. Gard. 26: 297. 1939. *C. sleumeri* Suess., Bot. Jahrb. Syst. 72: 282. 1942. Illustration: R. L. Wilbur & J. L. Luteyn, Ann. Missouri Bot. Gard. 65: 36, fig. 3. 1978 (as *Arctostaphylos*).

**Shrubs** or small **trees** to 20 m tall; twigs and petioles hirsute to ferruginously tomentose, the trichomes glandular or eglandular. **Leaves** with petioles pubescent; leaf blades usually densely ferruginous tomentose beneath, the midrib trichomes often glandular. **Inflorescences** with rachis, pedicels, bracts and bracteoles tomentose to glandular hirsute. **Flowers** with calyx tomentose, the lobes with glandular or eglandular pubescence; **corollas** glabrous to tomentose; ovary pubescent or more rarely glabrous.

Subspecies *arbutoides* ranges from the central highlands of Chiapas, Mexico to western Panama. In Costa Rica and Panama, it occurs in montane cloud forests (*Quercus*) and páramo, in the Cordillera de Talamanca of Costa Rica to western Panama (Chiriquí Prov., Volcán Barú), 1350–3800 m elevation. Flowering and fruiting occur throughout the year. The subspecies is characterized by ferruginous pubescence. The fruit is eaten in Honduras. The plants are visited by small, bumblebee-like Hymenoptera in Guatemala (Diggs, 1995). **Common**.

Subsp. **costaricensis** (Small) Diggs, Brittonia 38:

344. 1986. *Comarostaphylis costaricensis* Small, N. Amer. Fl. 29: 89. 1914. *Arctostaphylos costaricensis* (Small) Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 4: 320. 1929. *A. arbutoides* var. *costaricensis* (Small) Wilbur & Luteyn, Ann. Missouri Bot. Gard. 65: 36. 1978.

**Shrubs** to 5 m tall; twigs and petioles glabrous, often glaucous. **Leaves** glabrous beneath. **Inflorescences** glabrous or with slight pubescence. **Flowers** with calyx lobes, corollas, and ovary glabrous.

Subspecies *costaricensis* occurs in the montane cloud forest and in the dense ericaceous scrub vegetation at the edge of volcanic craters, 2500–3450 m elevation. It is endemic to Costa Rica, where it is abundant on the crater rim of Volcán Irazú (Cartago Prov.), and extends down into the forest of the Cordillera Central at Palmira (Alajuela Prov.) and Volcán Barva (Heredia Prov.). Flowering and fruiting occur throughout the year. The subspecies is characterized by its glabrous habit and often glaucous twigs and petioles. Common names in Costa Rica include *anonillo* (Heredia), *arrayán* (Cartago), and *madroño* (Cartago). **Locally Common**.

**Didonica Luteyn & Wilbur**

REFERENCES—J. L. Luteyn & R. L. Wilbur, New genera and species of Ericaceae (Vaccinieae)

from Costa Rica and Panama. Brittonia 29: 255–276. 1977. J. L. Luteyn, A synopsis of the genus *Didonica* (Ericaceae: Vaccinieae) with two new species. Syst. Bot. 16: 587–597. 1991.

Epiphytic **shrubs**, with mature stems glabrous to variously pubescent. **Leaves** alternate, petiolate, the blade coriaceous, flat to involute, margin entire or remotely crenate, the venation plinerved. **Inflorescences** axillary, flowers solitary or racemose; floral bract and bracteoles usually small and inconspicuous, margin glandular-fimbriate; pedicels continuous with calyx. **Flowers** 5–6-merous; calyx synsepalous, tube terete or apparently bluntly angled, limb usually terete and campanulate, lobes broad, relatively inconspicuous, erect; **corolla** sympetalous, aestivation valvate, thin or succulent, bistratose (in ours), cylindric-campanulate, usually greenish; **stamens** 10–12, equal; filaments distinct; connectives lacking disintegration tissue or spurs; anthers lacking awns, thecae finely papillate, incurved at base, tubules 2, distinct, rigid, slightly shorter than thecae, somewhat spreading, dehiscing by oval, latrorse clefts which do not extend to tip of tubule; pollen grains in tetrahedral tetrads, lacking viscin threads; ovary inferior; style filiform, about as long as corolla and included, or

slightly exserted, glabrous. **Fruit** a berry; seeds numerous.

*Didonica* consists of four species endemic to Panama and adjacent eastern Costa Rica. Virtually nothing is known about their biology, but the genus as a whole, as well as each of the four species, must be considered in extreme danger of extinction because the localities and habitats in which they are found are undergoing severe alteration. Only one species is currently known in Costa Rica. The morphological relationships of *Didonica* are presumed to be with genera such as *Macleania*, *Psammisia*, and *Mycerinus* because of similar short, broad, rigid anther tubules or with *Vaccinium* sect. *Oreades* Sleumer because of green flowers and sometimes latrorse anther dehiscence (Luteyn & Wilbur, 1977). As yet, there have been no DNA studies of this genus. *Didonica*, however, represents a rather distinct evolutionary line, and we are still unable to suggest with confidence its relationships to other Vaccinieae.

Key to the Species of *Didonica*

- 1a. Leaves imbricate, subsessile, clasping to amplexicaul, the blades deeply cordate at base, the margins entire; petioles to 2.5 mm long; mature stems hirsute; pedicels ca. 3 mm long . . . . *D. crassiflora*
- 1b. Leaves well separated, not imbricate, obviously petiolate, the blades short-attenuate or short-cuneate at base, the margins remotely crenate to essentially entire; petioles 5–15 mm long; mature stems glabrous or puberulent; pedicels (90) 150–205 mm long . . . . . *D. pendula*

***Didonica crassiflora*** Luteyn, Syst. Bot. 16: 592, fig. 4. 1991.

Epiphytic **shrubs**; mature stems subterete, striate, hirsute with white hairs 0.5–0.7 mm long, glabrate; twigs subterete, striate to ribbed, densely hirsute with white hairs to 1.5 mm long; axillary buds with outer pair of scales broadly ovate, mucronate, ca. 2 mm long. **Leaves** subsessile with petioles subterete, broadly canaliculate adaxially, to 2.5 mm long, 2.5–3 mm diam., densely hirsute; leaf blades coriaceous, densely imbricate, flat, amplexicaul with lobes slightly overlapping, ovate, 3.4–7 cm long, 1.7–3.7 cm wide, base rounded and deeply cordate, apex acuminate, sparsely hirsute over both surfaces and densely hirsute basally along nerves beneath, 5 (9)-plinerved from near base, midrib and inner 1–2 pairs of lateral veins impressed above and conspicuously raised beneath, outer 2 pairs of lateral veins plane to slightly raised above and beneath but obscure. **Inflorescences** with flowers solitary, surrounded at base by ca. 5 ovate, acute, marginally hirsute and glandular-fimbriate (inflorescence) bracts to ca. 1 mm long; floral bract ovate, ca. 1.5 mm long, apex acute to obtuse, sparsely short-pilose, margin with few, glandular fimbriae; pedicels subterete, broadening apically, ca. 3 mm long, ca.

1.5 mm diam., hirsute with white hairs ca. 1 mm long; bracteoles medial, ovate, ca. 1.5 mm long, densely pilose, apex acuminate. **Flowers** 6-merous; calyx 8–8.5 mm long, densely hirsute all over with white hairs to ca. 0.6 mm long, tube poorly developed, campanulate, ca. 2 mm long, ca. 4 mm diam., limb broadly campanulate, smooth, ca. 6 mm long, ca. 11 mm diam. at apical tip, lobes broadly deltate, 1.2–2 mm long, 3.5–4 mm wide at base, sinuses concave; **corolla** succulent when fresh, coriaceous, cylindric-campanulate, 14–15 mm long, 10–11 mm diam. at apical tip, pale green, nearly glabrous at base where covered by calyx limb but densely short-tomentose apically with pale, reddish, flat hairs to 0.7 mm long, lobes triangular-deltate, 3–3.5 mm long, ca. 4 mm wide at base, sparsely short-pilose within, apex acute; **stamens** 12, ca. 11 mm long; filaments 3–4 mm long, abaxially pilose; anthers 9.5–10 mm long, thecae 6.5–7.5 mm long, tubules ca. 3 mm long, dehiscing by oval clefts ca. 1.5 mm long; style slightly exserted, 15–16 mm long. **Berry** not seen.

*Didonica crassiflora* is known only from the type, which was collected along a stream on white, sandy soil with a very thin humus layer at the Fortuna Dam site, Chiriquí Province, Panama,

1200 m elevation. It has not yet been collected in Costa Rica. The type was flowering in February. **Endangered.**

*Didonica crassiflora* is characterized by its densely imbricate, amplexicaul leaves with hirsute blades; solitary flowers that are subsessile and 6-merous; hirsute calyces and pedicels; and tomentose, succulent corollas. It is morphologically similar to *D. subsessilis* Luteyn (endemic to Veraguas Prov., Panama), which is probably also its closest relative. Both species have short-petiolate, amplexicaul to clasping leaves, solitary flowers, and succulent corollas. They differ by *D. crassiflora* having mature stems hirsute (not glabrous); leaves amplexicaul with the blades flat and entire margined (not leaves clasping with blades flat to involute and margins remotely crenate); flowers 6-merous (not 5-merous); calyces and corollas hirsute and tomentose, respectively (not glabrous); and bracteoles inconspicuous and ca. 1.5 mm long (not conspicuous, concealing calyces and 7–8 mm long).

***Didonica pendula*** Luteyn & Wilbur, *Brittonia* 29: 255, fig. 1. 1977. Figure 2K.

Epiphytic **shrubs** 0.7–1 m tall, arising from a lignotuber; mature stems subterete, smooth or minutely striate, glabrous or puberulent; twigs subterete, striate, glabrous or puberulent; axillary buds with outer pair of scales narrowly ovate to linear-acicular, 2.5–5 mm long, long-acuminate. **Leaves** with petioles subterete, rugose, narrowly winged laterally over entire length, 5–15 mm long, 1.5–2 mm diam., glabrous; leaf blades coriaceous, slightly concave and bullate to flat, ovate to lanceolate-elliptic, (4.5) 6–18.5 cm long, (1.5) 2–5.4 cm wide, base rounded to obtuse and short-attenuate or short-cuneate, apex short- to long-acuminate, glabrous but bearing deciduous glandular fimbriae beneath, margin remotely crenate to essentially entire, weakly 5–7-plinerved (in ours) but appearing pinnately nerved with inner pair of lateral nerves arising about 1.5–4 cm above base, midrib conspicuous above in raised and thickened basal ca. 5 mm, then impressed apically, raised and prominent beneath, lateral nerves inconspicuous above, thin and slightly raised entire length, raised and conspicuous beneath, reticulate nerves slightly raised on both surfaces but somewhat conspicuous only beneath. **Inflorescences** with flowers solitary or in 1-flowered racemes, sometimes two racemes arising from same node, subtended by several, narrowly lanceolate to linear, long-acuminate bracts ca. 2 mm long; rachis (when present) subterete, thin, 1.5–10 mm long, the basal 1–2 nodes sterile; floral bract ovate, ca. 1–1.8 mm long, glabrous but margin glandular-fimbriate; pedicels long-pendent, minutely ribbed, (9) 15–20.5 cm long, 0.3–0.8 mm diam. throughout most of length, then greatly expanded apically near articulation to 5–8 mm diam. (15 mm diam. in fruit), glabrous; bracteoles 2.5–3 cm from base, subopposite, 1.5–4 mm long, aristate, glabrous, margin glandular-fim-

briate. **Flowers** 5–6-merous; calyx 8–12 mm long, glabrous, tube obconic, muricate, 3.5–5 mm long, ca. 4–5 mm diam. at base, limb campanulate, conspicuously veined, 3.5–7 mm long, ca. 12–13 mm diam. at apical tip, lobes broadly ovate, apiculate, 1–2.5 mm long, ca. 5 mm wide at base, sinuses acute to concave; **corolla** thin-carnose when fresh, bistratose, chartaceous, cylindric-campanulate, 16–25 mm long, 13–25 mm diam. at apical tip, glabrous, pink to greenish-white, lobes broadly ovate, 2.5–5 mm long, 5–6 mm wide at base, apex acute to rounded, glabrous internally; **stamens** 10 or 12, shorter than corolla, ca. 12–18 mm long; filaments ca. 4.5 mm long, ca. 2 mm wide at base, ciliate; connectives short-pilose; anthers ca. 10 (17?) mm long, thecae 6.5–7.5 mm long, tubules 3–3.5 mm long, pilose adaxially and on inner surfaces, dehiscing by oval clefts 1.5–2 mm long [authors unable to examine stamens from 25 mm long corolla]; style 16–18 mm long. **Berry** spherical, to 27 mm diam., translucent white.

*Didonica pendula* is distributed in eastern Costa Rica and west-central Panama, in cloud forest, 600–2600 m elevation. Five collections are known from Costa Rica (Limón Prov., Caribbean slope: road from Fila Dimat to Soki, *L. D. Gómez et al.* 23865; Zona Protectora Barbilla, SE of Siquirres, *M. Grayum et al.* 7946; and Sabanas de Durika, Parque Nacional La Amistad, Cerro Biricuacua, *G. Herrera* 6227. Puntarenas Prov., Pacific slope: Coto Brus, Zona Protectora Las Tablas, *E. Navarro* 838) and three from Panama. Flowering specimens have been collected in January, July, and October; fruiting specimens in January and October. **Endangered.**

*Didonica pendula* is characterized by leaves that are widely spaced and obviously petiolate, with blades basally broadly cuneate to short-attenuate and marginally remotely crenate to essentially entire; inflorescences with flowers solitary (or racemose but with only one flower maturing); and (usually) extremely long pedicels. The pedicels of some populations are the longest known in the Ericaceae, although one recent collection from Panamá Province, Panama, has pedicels 9.5–13 cm long. The six collections of this species show differences in twig pubescence, leaf size and shape, pedicel length, and number of flower parts. For example, the Panamanian populations (including the type) have thick-coriaceous, slightly concave, slightly bullate, ovate, short-acuminate leaf blades, 5.5–8.5 cm long, with the margins remotely crenate, and the venation conspicuously 5 (7)-plinerved with the inner pair of lateral nerves arising from near base. The Costa Rican populations have thin-coriaceous, flat, not bullate, lanceolate-elliptic, long-acuminate leaf blades, 10–18 cm long, with margins essentially entire, and

the venation obscure and appearing pinnate-nerved, with the inner pair of lateral nerves arising well above the base. We do not, however, consider these differences sufficient to warrant taxonomic recognition at this time. Additional collections are sorely needed.

Disterigma (Klotzsch) Niedenzu

REFERENCES—A. C. Smith, The genera *Sphyrrosperrum* and *Disterigma*. Brittonia 1: 203–232. 1933. R. L. Wilbur, A synopsis of the genus *Disterigma* (Ericaceae: Vaccinieae) in Mexico and Central America with the description of two previously undescribed species. Bull. Torrey Bot. Cl. 119: 280–288. 1992.

Compact, bushy to straggly, terrestrial or epiphytic shrubs. Leaves alternate, often congested, petiolate, the blade coriaceous, usually less than 3 cm long, the margin entire or crenate, the venation usually obscurely pliner-ved. Inflorescences axillary, of solitary or 1–6-clustered, subsessile flowers; floral bract 1 to several, minute, subcoriaceous; pedicels short or lacking, articulate with calyx; bracteoles 2, apical, immediately subtending and embracing calyx tube. Flowers (3) 4 (5)-merous, without odor, aestivation valvate (or rarely imbricate in

calyx); calyx tube campanulate to short cylindric, the lobes suberect; corolla sympetalous, subcylindric or campanulate-cylindric, (3) 4–5-lobed; stamens equal, (5–6) 8, usually twice as many as or rarely equal to corolla lobes; filaments distinct, ligulate, longer or shorter than anthers; connectives lacking disintegration tissue or spurs; anthers abaxially attached near base, membranous, lacking awns, thecae smooth, tubules 1 or 2, dehiscing by elongate, elliptical, introrse clefts or subterminal pores; pollen grains in tetrahedral tetrads, lacking viscin threads; ovary inferior, (3) 4 (5)-locular; style filiform, about as long as corolla or slightly exerted, glabrous; stigma truncate; nectariferous disc fleshy, annular-pulvinate. Fruit a thick-walled, coriaceous berry, blue-black or translucent white; seeds numerous, sometimes mucilaginous.

*Disterigma* is a genus of about 35 species distributed from southern Mexico to Bolivia and east to Guyana (Mt. Roraima). It is characterized by solitary or few-flowered clusters of sessile to sub- sessile flowers and two apical bracteoles that sub- tend the calyx tube and usually surround the entire calyx and sometimes also part of the corolla. The genus is morphologically most similar to *Vaccin- ium*, from which the bracteole feature distinguish- es it. Four species are currently known from Costa Rica. *Disterigma* is currently being revised in a Ph.D. study by L. Paola Pedraza (New York Bot- anical Garden).

Key to the Species of Disterigma

- 1a. Flowers 3-merous; corolla deep red; stamens 6 ..... *D. trimerum*
- 1b. Flowers 4-merous; corolla white (to pinkish), pale greenish, or red; stamens 8 or 10 ..... 2
  - 2a. Anther tubules 1; leaf blades with a terminal apiculus 1–2 mm long ..... *D. utleyorum*
  - 2b. Anther tubules 2; leaf blades not apiculate ..... 3
    - 3a. Leaf blades 4–20 mm wide, the apex rounded or obtuse (rarely acute); calyx tube 4-angled; calyx lobes eciliate; corolla 4.7–8 (14.5) mm long; flowers 1–3 per axil ..... 4
      - 4a. Leaf blades mostly 6–12 mm long, 4–7 mm wide; flowers mostly 1 (2 or 3) per axil; corolla 5–8 (14.5) mm long ..... *D. humboldtii*
      - 4b. Leaf blades mostly 15–30 mm long, 10–20 mm wide; flowers (1) 2 (3) per axil; corolla 4.7–7.5 mm long ..... *D. alaternoides*
    - 3b. Leaf blades 0.8–3 mm wide, the apex acute; calyx tube terete; calyx lobes ciliate; corolla 6–12 mm long; flowers always solitary ..... 5
      - 5a. Leaf blades 0.8–1.2 mm wide; calyx lobes ca. 1.5–2.2 mm long; corolla 6–8 mm long; staminal filaments 3.7–5 mm long ..... *D. fortuneense*
      - 5b. Leaf blades 1.5–3 mm wide; calyx lobes 2.5–3 mm long; corolla 10–12 mm long; staminal filaments 7–9 mm long ..... 6
        - 6a. Corolla lobes 2.2–3 mm long; leaf blades 1.5–2.2 mm wide, glabrous or at least glabrate; stamens 8, with filaments 7–9 mm long, twice as long as the anthers . . . . . *D. hammelii*
        - 6b. Corolla lobes ca. 1.5–1.7 mm long; leaf blades 2.5–4 mm wide, moderately short- pilose; stamens 10, with filaments ca. 7 mm long, less than 1.5 times longer than anthers ..... *D. pilosum*

**Disterigma alaternoides** (Kunth in H.B.K.) Niedenzu, Bot. Jahrb. Syst. 11: 224. 1889. *Vaccinium alaternoides* Kunth in H.B.K., Nov. Gen. Sp. 3: 265. 1818. *Metagonia alaternoides* (Kunth in H.B.K.) Nuttall, Trans. Amer. Phil. Soc. N.S. 8: 266. 1843.

Terrestrial or epiphytic shrubs 0.5–1.2 m tall (ours); mature stems terete or subterete, sometimes bluntly angled, nitid, glabrous; twigs subterete, angled, densely and finely spreading short-pubescent to hirsutulous with hyaline or grayish to brownish,  $\pm$  straight trichomes 0.2–0.6 mm long. **Leaves** with petioles subterete, stout and usually broadly flattened adaxially, 1–3 mm long, 1–1.5 mm diam., densely spreading short-pubescent; leaf blades coriaceous, with internodes mostly  $\frac{1}{5}$ – $\frac{2}{5}$  length of adjacent leaves, broadly elliptic, (15) 18–30 mm long, 10–20 mm wide, base rounded, apex obtuse to very broadly rounded or rarely acute, margin entire, glabrous or occasionally sparingly puberulous when young, also with inconspicuous appressed, amber-colored, glandular-fimbriae ca. 0.2 mm long beneath, obscurely 3–5-plinerved from base, midrib plane above and slightly raised beneath, lateral nerves usually plane above and slightly raised but usually obscure beneath, reticulate veinlets obscure on both surfaces. **Inflorescences** fasciculate, (1) 2 (3)-flowered (in ours); floral bract 1, semi-orbicular to broadly ovate, to 3 mm long, apex obtuse; pedicels subterete, ribbed, 2–3 mm long, puberulous to glabrate, sometimes also with scattered, minute, glandular fimbriae; bracteoles reaching to base of calyx lobes, imbricate at base, semi-orbicular, to 3 mm long, apex rounded, glabrous. **Flowers** 4-merous; calyx ca. 3–4 mm long, glabrous, tube cylindric, quadrangular, ca. 1.5 mm long, limb erect-spreading to campanulate, ca. 1.5 mm long, lobes deltate, ca. 1.6 mm long, apex acute, eciliate, sinuses acute; **corolla** thin-carnose, cylindric, ca. 4.7–7.5 mm long, 2–2.5 mm diam., glabrous or sometimes sparingly appressed puberulous, white, pinkish or pale red, to rarely even crimson, lobes deltate, 1.5–2 mm long, apex acute; **stamens** 8, ca. 6 mm long; filaments 2–4 mm long, densely hirsutulous; anthers 1.2–3 mm long, tubules 2, distinct, equaling or slightly exceeding thecae. **Berry** to 10 mm diam., translucent white or translucent pinkish, reddish-purple, or wine-red (unknown in our range).

*Disterigma alaternoides* ranges from Panama, south through the Andes to Bolivia, and east to Guyana and is found in premontane to montane cloud forest and páramo, (1600) 2400–3400 (3900) m elevation. It has not yet been found in Costa Rica. The Panamanian collections were flowering in March, April, June, and August (Wilbur, 1992). **Endangered** (if present).

*Disterigma alaternoides* is characterized by its broad, apically rounded to acute (in South America) leaves; inflorescences with usually paired, 4-merous flowers (in ours); and white to pinkish corollas. Morphologically it is most similar to *D. humboldtii*, with which it has in common broad

and usually rounded leaves, 4-merous flowers, and white corollas. The differences between these species are mentioned in the key, and although few, they do seem to hold within our range. Although mostly distributed in South America, *D. alaternoides* has been reported in Chiriquí Province, Panama (Wilbur, 1992). More collections are needed from Panama, and it may be possible that only one species, *D. alaternoides*, should be recognized.

**Disterigma fortuneense** Wilbur, Bull. Torrey Bot. Cl. 119: 286. 1992.

Epiphytic or terrestrial, erect to pendent **subshrubs** 0.3–0.4 m tall, often scrambling and rooting where stems touch moist soil; mature stems subterete, somewhat ridged and grooved, moderately to densely short-pilose with whitish to tawny trichomes 0.5–1 mm long, these especially dense at raised nodes; internodes very short, usually 1–2 mm long, mostly less than  $\frac{1}{8}$ – $\frac{1}{4}$  length of nearest leaf. **Leaves** with petioles 0.5–0.7 mm long, subterete, somewhat canaliculate adaxially, rugose, glabrous but appearing puberulous at base due to long nodal trichomes; leaf blades coriaceous, strongly spreading from stems often at about a right angle, needle-like, very narrowly linear, (4.5) 7–9 (11) mm long, 0.8–1.2 mm wide, 8–10 times as long as wide, base  $\pm$  rounded or very shortly tapering, apex acute, margin entire to very minutely serrulate, ciliate when young but becoming glabrous on both surfaces, obscurely 3–5-plinerved from near base although inner pair of lateral nerves arising ca. 2–3 mm above base, midrib and lateral nerves plane to weakly raised above but moderately weakly raised beneath, reticulate veinlets obscure. **Inflorescences** with flowers solitary; floral bracts ca. 5, to ca. 0.8 mm long, ovate,  $\pm$  orbicular to oblong, apex rounded, copiously short-ciliate, closely imbricate; pedicels ca. 1 mm long or less; bracteoles ca. 0.8–2 mm long,  $\pm$  orbicular or oblong, copiously short-ciliate, broadly imbricate and broadly clasping base of calyx. **Flowers** 4-merous; calyx ca. 3.2–4 mm long, tube ca. 1–1.8 mm long, ca. 1 mm diam., campanulate to somewhat globose,  $\pm$  terete, smooth, glabrous, limb spreading, ca. 1.6–2.2 mm long, lobes  $\pm$  erect, narrowly deltate to triangular-lanceolate, ca. 1.5–2.2 mm long, apex acute, ciliate in apical  $\frac{1}{2}$ – $\frac{2}{3}$  but otherwise glabrous, sinuses acute; **corolla** thin-carnose,  $\pm$  fusiform in bud but cylindric to somewhat infundibuliform when mature with base slightly tapering and mid- to apical swelling, 6–8 mm long, 2–3.6 mm diam., pink to white, essentially glabrous but with a few, apical trichomes, lobes triangular, 1–1.5 mm long, apex acute, strongly reflexed, with few microscopic trichomes; **stamens** 8, ca. 6 mm long, exerted from throat of corolla for ca. 1 mm; filaments 3.7–5 mm long, densely ciliate, obviously longer than anthers; anthers ca. 2.5–2.7 mm long, thecae slightly papillate, ca. 1–1.2 mm long, tubules 2, distinct, ca. 1.5–1.7 mm long, dehiscing by oblique, elongate pores; style exerted, ca. 8–8.5 mm long. **Berry** spherical, ca. 5.2 mm diam., translucent white with erect, persistent lobes.

*Disterigma fortuneuse* is a rare endemic in premontane cloud forest at the Fortuna Dam site of western Chiriquí Province, Panama, at ca. 1000–1100 m elevation. It has not yet been collected in Costa Rica and is known from only six collections. Flowering collections have been made in January and February; fruiting only in January. **Endangered.**

*Disterigma fortuneuse* is characterized by having needle-like, narrow leaves; small 4-merous flowers; and pink to white corollas. It belongs to a small group of species of *Disterigma* that normally have a scandent, "wiry", epiphytic habit; short internodes; and narrowly lanceolate to nearly linear leaf blades less than 5 mm wide. This group ranges from western Panama to central Peru and includes *D. agathosmoides* (Wedd.) Nied., *D. fortuneuse*, *D. hammelii*, *D. luteynii* Wilbur, *D. panamense* Standley, *D. pilosum*, and *D. weberbaueri* Hoerold. Apparently *D. fortuneuse* is most closely related to the South American (Colombia and Ecuador) *D. agathosmoides*, and more collections and field observations are needed to distinguish the species. One collection (*Luteyn 14808*, NY) was associated with stinging ants.

***Disterigma hammelii* Wilbur & Luteyn, Ann. Missouri Bot. Gard. 68: 160. 1981.**

Straggly, pendent, epiphytic **shrubs**; mature stems thin, subterete, irregularly ridged and grooved, moderately spreading to appressed short-pilose with hyaline to tawny trichomes; twigs subterete, angled, ridged, densely spreading short-pilose with tawny to reddish-brown trichomes 0.4–1 mm long; internodes short, almost all less than  $\frac{1}{4}$  length of subtending leaves and usually 1–2 mm long. **Leaves** with petioles subterete, flattened adaxially, 0.5–1 mm long, glabrous or nearly so; leaf blades coriaceous, elliptic to lance-elliptic, (4) 5–7 (8) mm long, 1.5–2.2 (3) mm wide, mostly about 2.5 times as long as wide, base gradually tapering into petiole, apex acute in general outline but actual apex obtuse, margin entire, glabrate on both surfaces and margin or ciliolate at apex, rarely with a few appressed, reddish, glandular fimbriae on lower surface, venation indistinct except midvein slightly elevated beneath. **Inflorescences** axillary, of solitary flowers; floral bracts 5–8, mostly 0.8–1.8 mm long, ovate to broadly elliptical, tawny to dull reddish-brown, scarious; pedicels ca. 0.5–0.8 mm long, glabrous, obscured from view by bracts and bracteoles; bracteoles broadly clasping, covering calyx to base of lobes, ovate to broadly oblong, striate, apparently concave, 2–2.7 mm long, ca. 2–2.5 mm wide, apex broadly rounded, margin scarious. **Flowers** 4-merous; calyx ca. 3.8–4 mm long, glabrous to sparingly short-pilose, tube terete, campanulate to obconic, ca. 1.4–1.8 mm long, 1–1.4 mm diam., limb spreading, ca. 2.8–3.3 mm long, lobes strongly ascendent, striate, narrowly lanceolate with incurved margin, ca. 2.5–3 mm long, apex

acute, margin entire, ciliate for apical  $\frac{1}{3}$ – $\frac{1}{2}$  but otherwise glabrous, sinuses acute; **corolla** cylindric, sometimes somewhat quadrate, 10–12 mm long, 2.5–3.2 mm diam., pale pink, nearly glabrous but usually with a few, appressed, glandular trichomes ca. 0.1 mm long just above middle, lobes ascendent to more typically reflexed, 2.2–3 mm long, lanceolate, acute, spreading, short-pubescent with hyaline trichomes; **stamens** 8, ca. 10–11 mm long, about as long as corolla; filaments ca. 7–9 mm long, conspicuously longer than anthers, sparingly hyaline short-pilose with trichomes 0.2–0.6 mm long; anthers ca. 3.7–4.3 mm long, thecae ca. 1.2–1.5 mm long, tubules 2, distinct, ca. 2.5–2.8 mm long; style exserted, ca. 13–14 mm long, glabrous. **Berry** not seen.

*Disterigma hammelii* occurs in montane and Continental Divide cloud forest, 1800–2200 m, and is known only from three collections in Chiriquí-Bocas del Toro Provinces, Panama. It has been collected near but not yet within the borders of Costa Rica. Flowering specimens have been collected in February and March; fruits are unknown. **Endangered.**

*Disterigma hammelii* also belongs with those *Disterigma* species that normally have a scandent, "wiry," epiphytic habit; short internodes; and narrowly lanceolate to nearly linear leaf blades less than 5 mm wide, as mentioned in the discussion above. From this group *D. hammelii* may be distinguished by its longer corolla, especially its proportionally long staminal filaments, and by its exserted style.

***Disterigma humboldtii* (Klotzsch) Niedenzu, Bot. Jahrb. Syst. 11: 224. 1889. *Vaccinium humboldtii* Klotzsch, Linnaea 24: 57. 1851. *V. pachyphyllum* Hemsl. Biol. Centr.-amer., Bot. 2: 275. 1881. *D. pachyphyllum* (Hemsl.) S. F. Blake, J. Washington Acad. Sci. 16: 365. 1926. Figures 2U and 3.**

Bushy, compact to straggly, terrestrial or epiphytic **shrubs** (0.2) 0.5–1 (1.2) m tall; mature stems terete to subterete, sometimes conspicuously ribbed and bluntly angled due to raised nodes; twigs subterete, bluntly angled, striate, densely short-pilose to setose with ferruginous to brown hairs 0.5–1.2 mm long, or moderately to densely puberulent, glabrate. **Leaves** with petioles subterete, broadly flattened adaxially, 1–2 mm long, weakly to moderately short-pilose and this sometimes onto base of midrib beneath; leaf blades coriaceous, ovate, elliptic, to suborbicular, revolute near base, 6–12 (16) mm long, 4–7 (9) mm wide, base rounded, apex obtuse to rounded, margin entire, sometimes with a dense but short, tuft of hairs at apex, otherwise glabrate, also bearing scattered, appressed, glandular fimbriae beneath to ca. 0.2 mm long, obscurely 3-plinerved from base, midrib slightly impressed above and sometimes slightly raised beneath, all other venation completely obscured on both surfaces. **Inflorescences** of solitary flow-



ers or 2–3 in a fascicle; floral bract 1 (3), ovate, less than 1 (2.2) mm long; pedicels to 2 mm long, glabrous; bracteoles clasping calyx to base of lobes, broadly oblong-ovate, 1.5–4 mm long, broader than long, apex rounded to truncate. **Flowers** 4-merous; calyx ca. 3.3 mm long, glabrous, tube campanulate, 4-angled, ca. 1 mm long, limb spreading, 2–3.5 mm long, lobes erect to slightly spreading, ovate-deltate, 1.3–2.5 mm long, apex acute, glabrous or sparsely appressed pubescent to ciliate, sinuses acute; **corolla** thin-carnose, cylindric, 5–8 (14.5) mm long, 2–4 (5) mm diam., glabrous to sparingly appressed pilose externally and rarely moderately short-pilose internally, white or sometimes suffused with rose or pink, lobes erect to horizontally spreading, deltate, ca. 1 mm long, apex acute; **stamens** 8, 5.8–11.5 mm long, about equaling corolla but often exposed at anthesis when corolla lobes become reflexed; filaments 2.5–4.5 (7.5) mm long, moderately to densely hispidulous to appressed pilose (or villous) in apical half with whitish or hyaline hairs; anthers 2.4–5.5 mm long, thecae 1.2–2 mm long, tubules 2, distinct, 1.3–3.5 mm long, dehiscent by elongated clefts about half the tubule length; style slightly exserted, glabrous. **Berry** spherical, crowned by persistent calyx limb, ca. 5 mm diam., translucent white to translucent purple.

*Disterigma humboldtii* is found in premontane cloud forest to subpáramo, and pastures, 300–3200 m elevation, from Mexico to Ecuador and east to Guyana. In Costa Rica it is encountered in the cordilleras Tilarán, Central and Talamanca. Flowering occurs throughout the year; fruiting specimens have been collected in July, October, and December. **Widespread.**

*Disterigma humboldtii* is characterized by its apically obtuse to rounded leaf blades, usually 1 (3)-flowered inflorescences, and 4-merous flowers. The relationships of *D. humboldtii* lie near *D. alaternoides* as discussed above. The berries are reportedly sweet. Flowers are visited by hummingbirds (J.L.L., pers. observ.), but bees are probably the primary pollinators.

***Disterigma pilosum* Wilbur, Bull. Torrey Bot. Cl. 119: 285. 1992. Figure 4.**

Pendent, densely clustered, epiphytic **shrubs**; mature stems subterete, angled to ribbed, swollen at nodes; twigs subterete, angled, striate, densely spreading short-pilose with tawny hairs 1–1.2 mm long, the new innovations with persistent, striate, oblong, apically obtuse to rounded, ciliate perulae to 4 mm long; internodes short, almost all less than  $\frac{1}{4}$  length of nearby leaves, mostly 2–6 mm long. **Leaves** with petioles subterete, 0.5–1.5 mm long, sparingly to moderately short-pilose; leaf blades coriaceous, thick when fresh but puckering and wrinkling on drying, elliptic to lance-elliptic, 8–15 mm long, 2.5–4 mm wide, mostly 3–4 times as long as wide, base gradually tapering and rounded, apex tapering to a blunt tip, margin entire, moderately short-pilose on both surfaces and margins, obscurely 3-plinerved

from base, midrib and lateral nerves sometimes obscure above but raised beneath, reticulate nerves obscure above but slightly raised beneath. **Inflorescences** axillary, of solitary flowers; floral bracts 5–9, ovate to broadly orbicular, apex rounded, glabrous to short-pilose to minutely ciliate, scarious, mostly 0.6–1.5 mm long, concealing pedicel; pedicels ca. 0.4–1.5 mm long; bracteoles broadly clasping, broadly ovate to ovate-oblong or  $\pm$  orbicular, 1.8–3 mm long, apex rounded, margin scarious, ciliate. **Flowers** 4-merous; calyx ca. 4.2–4.5 mm long, somewhat striate, sparingly puberulous to short-pilose, tube terete, obconic, ca. 1.5 mm long, limb ca. 2.7–3 mm long, lobes erect or strongly ascendent, narrowly lanceolate, acute with incurved margins, 2.5–3 mm long, sinuses acute; **corolla** cylindric to somewhat swollen medially, 10–12 mm long, 1.5–3 mm diam., sparingly short-pilose externally, whitish to pale pink, lobes erect to somewhat reflexed, lanceolate, acute, 1.5–1.7 mm long; **stamens** 10, ca. 12 mm long; filaments ca. 7 mm long, longer than anthers, swollen at base, scattered long-pilose in apical  $\frac{1}{2}$ ; anthers ca. 5 mm long, thecae ca. 1.5 mm long, tubules 2, distinct, ca. 3.5 mm long, dehiscent by clefts ca. 1.5 mm long. **Berry** not seen.

*Disterigma pilosum* is found on the wet Caribbean slope of the Continental Divide in *Quercus* forest, 2300–2700 (3000) m elevation. It is endemic to the Cordillera de Talamanca near the Costa Rica/Panama border and is known only from three collections: Limón Province, Costa Rica (*Davidse et al.* 28937 and *Morales* 5801), and Bocas del Toro Province, Panama (*T. Antonio* 1630, sterile). Flowering specimens have been collected in September; fruits are unknown. **Endangered.**

*Disterigma pilosum* is characterized by its generally dense to moderately short-pilose, narrow elliptic to lance-elliptic leaf blades; 4-merous flowers with relatively long (2.5–3 mm) calyx lobes; and 10 stamens (not the normal eight). *Disterigma pilosum* is seemingly related to those species of *Disterigma* that normally have a scandent, “wiry” epiphytic habit; short internodes; and narrowly lanceolate to nearly linear leaves less than 5 mm wide, as mentioned in the discussion of *D. fortuneense* above. It keys closest to *D. hammelii*, but until more collections of these taxa are made, their relationships are uncertain.

***Disterigma trimerum* Wilbur & Luteyn in Luteyn & Wilbur, Brittonia 29: 258. 1977.**

Epiphytic or terrestrial, bushy **shrubs** 0.5–1.5 (2) m tall to small trees ca. 4 m tall (fide label); mature stems terete to subterete, conspicuously fissured, glabrous; twigs subterete, sharply ridged and grooved, indistinctly 3-angled to irregularly 4-angled, glabrous or minutely puberulous, sparingly glandular-fimbriate; internodes  $\frac{1}{5}$ – $\frac{2}{3}$  as long as the surrounding leaves. **Leaves** with



petioles subterete, broadly canaliculate adaxially, 3–5 mm long, glabrous to puberulent; leaf blades coriaceous, broadly elliptic to somewhat obovate or spatulate, (0.8) 1.2–2 cm long, (4) 6–14 mm wide, base cuneate, apex obtuse to broadly rounded, short-retuse, margin entire to obscurely serrulate, glabrous above, evenly but sparingly bearing appressed, amber to reddish-brown, glandular fimbriae 0.2–0.3 mm long beneath, 3–5-plinerved from near base, midrib and lateral nerves raised (sometimes conspicuously) basally but nearly plane apically above, raised (sometimes conspicuously) beneath but often obscure on both surfaces, reticulate veinlets slightly raised but usually obscure on both surfaces. **Inflorescences** axillary, of solitary (rarely 2), subsessile flowers; floral bract 1, triangular-acuminate to deltate or acutely oblong, to ca. 1.5 mm long, ca. 1.5 mm wide, glabrous or ciliate, margin glandular-fimbriate; pedicels 2–3 mm long, densely glandular-fimbriate at articulation; bracteoles 1.5–1.8 mm below base of calyx tube, subopposite, imbricate, broadly clasping, semi-orbicular, ca. 1.5–2.5 mm long, 1.8–2 mm wide, scarcely overlapping base of calyx tube, ciliate, margin glandular-fimbriate. **Flowers** 3-merous; calyx ca. 4–5 mm long, glabrous, tube terete, cylindric, ca. 2–3.5 mm long, 2–2.5 mm diam., limb spreading, smooth, ca. 1.5–2.5 mm long, lobes erect, broadly deltate, ca. 0.5–1.3 mm long, apex acute, eciliate, sinuses concave; **corolla** carnose, bistratose, cylindric but abruptly tapering at base, 5.6–9 mm long, 2.5–4 mm diam., deep red, glabrous but sometimes bearing few, ascendent, glandular fimbriae to 0.1–0.2 mm long in basal half, lobes erect, oblong-deltoid, 1.5–2 mm long, 1–1.2 mm wide, apex acute; **stamens** 6, ca. 7 mm long, shorter than corolla; filaments distinct, ca. 2.5–3.5 mm long, glabrous; connectives sometimes sparsely pilose along margin; anthers ca. 4.8–5.3 mm long, thecae 2.3–2.8 mm long, tubules 2, distinct, 2.5–2.8 mm long, dehiscing by introrse, elongate, oval slits ca. 1.5 mm long; style equaling corolla or slightly exserted. **Berry** at first greenish-white turning dark blue (in two collections reportedly translucent white).

*Disterigma trimerum* is endemic to the premontane, wet montane, and Continental Divide forest in eastern Costa Rica and western Panama, (1100) 1500–2240 m elevation. It has been collected only twice in Costa Rica (Limón Prov., Dto. Bratsi, Cordillera de Talamanca, Caribbean slopes, Cuenca del Sixaola, area of Río Lari and Río Coén, *Bittner 1816* and *Aguilar 1157*). Flowering specimens have been collected in January–July; fruiting in January–February and May–July. **Endangered.**

*Disterigma trimerum* is characterized by having usually obovate, serrulate leaf blades with rounded and shortly retuse tips; broadly clasping, semi-orbicular bracteoles that are located below the apex of the pedicel and scarcely reach the base of the calyx tube; and 3-merous flowers with deep red corollas. The trimerous flowers are unknown anywhere else in *Disterigma*. Herbarium specimens indicate that mature fruit color varies from

generally dark blue to rarely translucent white; this needs further investigation. Morphological and molecular studies show that *D. trimerum* is isolated from all other species in the genus.

***Disterigma utleyorum*** Wilbur & Luteyn in Luteyn & Wilbur, *Brittonia* 29: 259. 1977. Figure 7.

Epiphytic *shrubs* 20–45 cm tall; mature stems terete, glabrous; bark cracking irregularly and exfoliating in thin strips; twigs subterete to terete, moderately to densely puberulent. **leaves** congested, with petioles subterete, flattened adaxially, 1–2 (4) mm long, puberulent; leaf blades thick and fleshy when fresh but becoming thin and wrinkled when dry, oblong, obovate, somewhat spatulate, or rarely oblong-elliptic, slightly revolute, (1) 1.5–2.5 (3) cm long, (0.7) 1–1.8 cm wide, base broadly cuneate to obtuse, apex obtuse to broadly rounded, with a deciduous or persistent, weakly short-pilose apiculum 1–2 mm long, margin entire, both surfaces minutely puberulent but also with minute, glandular fimbriae ca. 0.1 mm long, 5 (7)-plinerved from base, midrib and lateral nerves conspicuously raised above and beneath, reticulate veinlets slightly raised on both surfaces. **Inflorescences** axillary, of solitary, subsessile flowers; floral bract apparently 1, ovate, ca. 0.5–1.5 mm long, apex rounded, puberulent, ciliate; pedicels subterete, striate, 0.5–2 mm long; bracteoles subopposite, fused below into a cupule 0.5–1 mm long that loosely surrounds the basal part of the calyx tube, broadly oblong to ovate, 1.5–2 mm long, 2–3 mm wide, minutely appressed puberulous. **Flowers** 4-merous; calyx ca. 4.5–5.5 mm long, tube cylindric, ribbed, 2–3 mm long, puberulous, limb campanulate, 1–3 mm long, lobes erect, lanceolate to narrowly triangular, 1.5–2.2 mm long, ca. 1 mm wide at base, apex acute to acuminate, minutely puberulous, sinuses acute; **corolla** thin-carnose, somewhat funnelliform or cylindric-campanulate, 5.5–10 mm long, 3.5–9 mm apical diam., white, glabrous but sparingly glandular-fimbriate, lobes oblong-elliptic to broadly deltate, 3.5–5 mm long, ca. 3–4 mm wide, apex acute; **stamens** 8, ca. 5–6 mm long, about half as long as corolla; filaments 1.5–2.5 mm long, weakly ciliate; anthers 2.5–4.5 mm long, minutely papillate over entire thecae and apically onto base of tubules, thecae 1.5–2.5 mm long, basally shortly appendiculate, tubule 1, ca. 1–2.3 mm long, dehiscing by a single, obliquely-terminal, circular pore; style 4.8–5.3 mm long. **Berry** spherical, ca. 7 mm diam., translucent white.

*Disterigma utleyorum* is found in lowland rainforest to premontane cloud forest, seemingly in the tops of large trees, (450) 700–1200 m elevation. It is a rare species, and is sporadic in its distribution, having been collected twice from one locality in Costa Rica (vicinity of Cariblanco, Heredia Prov.), once in Panama (Prov. Veraguas), once in Colombia, and about six times from four localities in Ecuador. Flowering specimens have been collected in February–May, August, Octo-

ber, and November; fruiting in August and October. **Endangered.**

*Disterigma utleyorum* is easily identified and is unique in the genus in its combination of obovate to spatulate leaf blades that are basally cuneate and 5-plinerved, inflorescences with solitary, 4-merous flowers, and anthers with a single tubule. Its relationships within the genus are obscure. In Costa Rica and Ecuador (perhaps everywhere?), *D. utleyorum* always seems to be associated with colonies of biting ants; furthermore, the mature stems seem to radiate from a large, moist ball of earth and vegetable debris 30 cm or so in diameter capped by a dense, mat-forming acrocarpous moss. The details of this intriguing commensal relationship between ericad and insect are at present unknown.

## Gaultheria Linnaeus

REFERENCE—J. L. Luteyn, *Gaultheria*. Fl. Neotrop. Monogr. 66: 384–488. 1995.

Erect **shrubs** (in ours), prostrate undershrubs, or rarely small trees; indumentum of simple, unicellular or multiseriate, multicellular eglandular or gland-tipped hairs. **Leaves** alternate, evergreen, petiolate, the blades usually coriaceous, the margin usually serrate or crenate, the venation pinnate. **Inflorescences** axillary, racemes or flowers solitary, these then multibracteate at base; pedicels articulate with calyx and subtended by a single floral bract; bracteoles 2 to several, basal to apical. **Flowers** 5-merous, without odor; calyx synsepalous, lobed nearly to base, usually fleshy and accrescent after anthesis; **corolla** sympetalous, aestivation imbricate, urceolate to campanulate, or sometimes cylindric-urceolate, white to pinkish or reddish; **stamens** 10, ca.  $\frac{1}{2}$ – $\frac{2}{3}$  corolla length; filaments distinct, glabrous or pubescent; connectives with disintegration tissue along connective and onto awns, lacking spurs; anthers bilocular, each loc-

ule dehiscent introrsely by an apical pore and with 2, terminal, papillate awns, thecae papillate, tubules lacking; pollen grains in tetrahedral tetrads, lacking viscin threads; ovary superior, 5-locular; ovules 5–10; style about as long as corolla. **Fruit** a 5-valved, loculicidal capsule surrounded by the usually white or dark blue-black, fleshy, accrescent calyx; seeds numerous, ca. 1–1.5 mm long, wingless.

*Gaultheria* consists of ca. 115 species distributed in a circum-Pacific ring from Japan and China; south through Malesia, southern Australia, and New Zealand; and then from the southern tip of South America north through the Andes, Mesoamerica, the West Indies, and to the U.S.A. and Canada. There are two species in Costa Rica. *Gaultheria* is characterized by a superior ovary and capsular fruit. At maturity the capsule is completely surrounded by a fleshy, accrescent calyx; thus, the dispersal unit appears berry-like. The genus is traditionally distinguished from *Pernettya* by its capsular fruit (vs. a true berry in *Pernettya*). Furthermore, the calyx of *Pernettya* normally remains dry and basal to the berry. Although the tips of the calyx lobes of *Pernettya* sometimes become fleshy, the calyx always remains small, distinct, and located at the base of the berry, never accrescent and surrounding it (Luteyn, 1995). Several recent authors have chosen to unite *Pernettya* under *Gaultheria*, reasoning that in all other morphological characters (save the calyx and fruit features), *Pernettya* is not distinct from *Gaultheria* (Stevens, 1971; Middleton & Wilcock, 1990; Kron et al., 2002a; Stevens et al., 2004). Molecular data are somewhat inconclusive, and too few taxa have been examined; however, the studies of Powell and Kron (2001) and Kron et al. (2002a) do support the inclusion of *Pernettya* within *Gaultheria* s.l. In this treatment of the Costa Rican Ericaceae, we maintain the genera as distinct.

## Key to the Species of *Gaultheria*

- 1a. Branchlets conspicuously strigose with straight, rigid, appressed (more or less spreading) hairs; leaf blades appressed-strigose beneath, elliptic to ovate-elliptic; indumentum eglandular . . . *G. gracilis*
- 1b. Branchlets glabrous to densely white puberulent and also moderately to densely hirsute; leaf blades glabrous to moderately hirsute beneath, elliptic to subrotund; indumentum eglandular to glandular . . . . . *G. erecta*

***Gaultheria erecta*** Vent., Descr. Pl. Nouv. 5, pl. 5. 1800. *G. odorata* Bredem. ex Willd., Ges. Naturf. Freunde Berlin Neue Schriften 3: 425. 1801. *Brossea erecta* (Vent.) Kuntze, Rev. Gen.

Pl. 2: 388. 1891. *G. odorata* Kunth in H.B.K., Nov. Gen. Sp. 3: 285. 1819, non Bredem. ex Willd. (1801). *Brossea odorata* (Kunth in H.B.K.) Kuntze, Rev. Gen. Pl. 2: 388. 1891. *G.*

*odorata* Kunth in H.B.K. var. *costaricensis*, J. D. Smith, Bot. Gaz. 20: 292. 1895. *G. costaricensis* (J. D. Smith) Small, N. Amer. Fl. 29: 79. 1914. *G. glandulifera* Small, N. Amer. Fl. 29: 78. 1914. *G. donnellii* Sleumer, Notizbl. Bot. Gart. Berlin-Dahlem 12: 125. 1934. *G. poasana* Sleumer, Notizbl. Bot. Gart. Berlin-Dahlem 12: 127. 1934. *G. subrotunda* Sleumer, Notizbl. Bot. Gart. Berlin-Dahlem 12: 284. 1935. Figures 1E and 8.

Terrestrial, erect to arching or spreading, rhizomatous, **shrubs** to 3 m tall, often epiphytic in Costa Rica; mature stems sometimes glaucous, glabrous to sparsely white puberulent, also often persistently hispid-hirsute with eglandular or gland-tipped hairs. **Leaves** with petioles 1–8 mm long, puberulent (glabrate) and often hirsute with eglandular or gland-tipped hairs; leaf blades flat to sometimes bullate, sometimes clasping, ovate, elliptic, to subrotund, (2) 5–11 cm long, (1) 2.5–6.5 cm wide, base rounded to broadly cuneate, often subcordate to deeply cordate, apex acute or short-acuminate, glabrous to puberulent along veins above, also sparsely or moderately hirsute on lamina or veins with often gland-tipped hairs, sparsely to densely hirsute beneath with eglandular or minutely gland-tipped hairs, both surfaces often glabrate, margin remotely and shallowly crenate-serrate, pinnately veined. **Inflorescences** axillary, racemose, 10–26-flowered; rachis 2–12 cm long, moderately to densely puberulent, also moderately to densely hirsute with eglandular or gland-tipped hairs; floral bract concave, cochleariform, ovate to ovate-elliptic or obovate, (3.7) 8–16 mm long, (1.6) 3–6 mm wide, apex acute to acuminate, sparsely puberulent, margin sparsely ciliolate and often glandular-pubescent, white to pale greenish or sometimes tinted with rose; pedicels (3) 8–13 mm long, pubescent as rachis; bracteoles basal or medial, narrowly elliptic-ovate to linear-ovate, (1.5) 5–7 mm long, (0.5) 1–1.5 mm wide, apex long-acuminate, weakly puberulent, margin ciliolate, often bearing gland-tipped hairs. **Flowers** with calyx (3) 4–6 (9) mm long, glabrous to densely puberulent, sometimes glabrate, also often moderately to densely hirsute with eglandular or glandular setae, lobes (1.5) 3–5.5 (7) mm long, erect to sometimes reflexed, triangular to ovate, acute to long-acuminate, densely ciliolate; **corolla** ovate-urceolate to cylindric-urceolate, (4.5) 6–7 (8) mm long, 3–4.6 mm diam., glabrous to sparsely or densely short-pilose, also often sparsely to densely hirsute to strigose with eglandular or gland-tipped hairs, white to red; **stamens** (2.7) 5–6 mm long; filaments (2.1) 3.5–5 mm long, pilose; anthers 1.2–2.8 mm long, awns short and sometimes inconspicuous; ovary glabrous to densely short-pilose. **Fruiting** 7–12 (15) mm diam., glabrous to sparsely pilose, sometimes also sparsely hirsute with gland-tipped hairs, blue-black.

*Gaultheria erecta* is found in open or shrubby areas such as road banks, landslides, or meadows; rocky places; montane and *Quercus* forest; edges of cloud and elfin forest; páramo and subpáramo thickets; and rarely in boggy areas, (1200) 2000–3200 (3700) m elevation (in Costa Rica). It has

the broadest geographical range of any species in the genus, being distributed from north-central Mexico through Central America into the Andes of South America to northern Argentina and also rarely in southeastern Brazil. In Costa Rica it is commonly found as an epiphyte (less frequently terrestrial), whereas in the rest of its range it is always found as a terrestrial shrub. Flowering and fruiting occur throughout the year. **Common.**

In Costa Rica, *Gaultheria erecta* is characterized by its usually epiphytic habit, large leaves with blades that are oblong-elliptic and nitid, superior ovary, and capsular fruit that is surrounded by fleshy, accrescent calyx lobes.

The relationships of *Gaultheria erecta* are uncertain, but it is morphologically similar to several South American species, including *G. rigida* Kunth, *G. santanderensis* A. C. Smith, *G. hapalotricha* A. C. Smith, and *G. setulosa* N. E. Brown. Within Central America, it is morphologically most similar to the Panamanian endemic *G. chiriquensis* Camp, a species that is not expected in Costa Rica. From the only other species of *Gaultheria* in Costa Rica and adjacent western Panama, *G. gracilis*, with which it may be remotely related, it is easily distinguished by the characters mentioned in the key. In South America, *Gaultheria erecta* apparently hybridizes with *Pernettya prostrata* and several other species of *Gaultheria* (see Luteyn, 1995), but thus far there is no evidence for hybridization in Costa Rica. Fruits are eaten by birds.

***Gaultheria gracilis*** Small, N. Amer. Fl. 29: 77. 1914. *G. barbata* Small, N. Amer. Fl. 29: 77. 1914. *G. setosa* Small, N. Amer. Fl. 29: 77. 1914. *G. gracilis* Small var. *intermedia* Sues-senguth & Goepfinger, Bot. Jahrb. Syst. 72: 282. 1942, nom. nud. Illustration: R. L. Wilbur & J. L. Luteyn, Ann. Missouri Bot. Gard. 65: 86, fig. 8. 1978. Figure 8.

Terrestrial or sometimes epiphytic **shrubs** 0.4–2 m tall; mature stems glabrous, but twigs moderately to densely appressed-strigose with eglandular hairs, often glabrate. **Leaves** with petioles 4–7 mm long, strongly canaliculate adaxially, short-puberulent and glabrate, often also strigose; leaf blades flat or somewhat bullate, elliptic to ovate-elliptic, (3) 4–6 (8.5) cm long, (1) 1.5–2.5 (3.5) cm wide, base acute or cuneate to obtuse, apex long-acuminate to acute, sparsely to densely appressed strigose above with deciduous hairs, conspicuously and usually densely appressed strigose beneath, margin minutely serrulate with each tooth terminating in an appressed bristle, pinnately nerved. **Inflorescences** racemose, 6–9 (14)-flowered; rachis (2) 3–7 (8) cm long,

moderately to densely white-short-pilose or densely strigose with usually eglandular hairs; floral bract apparently continuous with pedicel, conspicuously striate, cucullate, strongly divergent, elliptic to spatulate, 3–10 (14) mm long, ciliate, puberulous or glabrous; pedicels 5–10 (12) mm long, moderately to densely white-short-pilose; bracteoles apparently continuous with pedicel, medial, linear to narrowly oblong, 2–4.5 mm long, ciliate and sometimes densely short-pilose. **Flowers** with calyx 3.5–5 mm long, glabrous or rarely densely strigose, lobes 2–3 mm long, ovate to deltoid, acute to acuminate, ciliate; **corolla** urceolate to cylindric-urceolate, 4–8 mm long, 3–4.3 mm diam., glabrous or moderately to densely strigose, rarely strigose with eglandular or minutely gland-tipped hairs, greenish or white to rose; **stamens** 2.3–3 mm long; filaments 1.5–2.2 mm long, glabrous or weakly pilose; anthers 1–1.3 mm long, awns prominent; ovary glabrous or weakly short-pilose. **Fruiting** to 9 mm diam., glabrous, blue-black.

*Gaultheria gracilis* is found in cloud and elfin forests, high-elevation bogs, disturbed forest, and remnant trees in pasturelands, (1100) 1400–2700 (3150) m elevation. It is endemic to Costa Rica and adjacent western Panama. Flowering specimens have been collected in January, February, June, July, and October–December; fruiting in February, June–August, and December. **Wide-spread.**

*Gaultheria gracilis* is characterized by having strigose branches, long-acuminate leaf blades, strongly canaliculate petioles, densely white pilose rachises and pedicels, and linear and medially located bracteoles. The plants are said to be small trees in boggy areas, but no heights have been given on herbarium labels. There is some variation in its indumentum. The branches, which are normally appressed strigose, may have spreading hairs (= *G. barbata*), or the corolla may be glabrous (= *G. setosa*) to densely strigose, but these variations are matters of degree and may often occur within populations. *Gaultheria gracilis* is morphologically most similar to *G. strigosa* Benth and *G. insipida* Benth, both from South America. There is a somewhat remote relationship with *G. erecta*, also found in Costa Rica, as in-

dicated by a similarity in the shape and texture of the floral bracts.

## Gonocalyx Planch. & Lindl.

REFERENCES—J. L. Luteyn, Notes on Neotropical Vaccinieae (Ericaceae). I. *Gonocalyx*—a genus new to Central America. *Brittonia* 28: 37–41. 1976; J. L. Luteyn, *Gonocalyx amplexicaulis* (Ericaceae): A new Panamanian blueberry. *Syst. Bot.* 15: 745–747. 1990.

Epiphytic **shrubs**, rarely small terrestrial trees or herbs. **Leaves** alternate, sessile to petiolate, the blade coriaceous, flat to revolute, with margin entire or crenate, the venation obscurely plinerved. **Inflorescences** axillary, flowers solitary, in pairs, or in loose, few-flowered racemes; floral bract small; pedicels articulate with calyx; bracteoles 2, usually basal. **Flowers** (4) 5-merous; calyx synsepalous, tube terete, bluntly angled, or narrowly winged opposite the sinuses, lobes apiculate; **corolla** sympetalous, aestivation valvate, membranous to thinly carnose, usually bistratose, tubular, subcylindric, cylindric-campanulate, or globose-urceolate; **stamens** 10, equal (rarely apparently alternately unequal), nearly as long as the corolla; filaments distinct or connate; connectives lacking disintegration tissue or spurs; anthers lacking awns, thecae minutely papillate, tubules 2, distinct, longer and thinner than thecae, dehiscent by introrse, minute, subterminal, oblique pores or short slits; pollen grains in tetrahedral tetrads, lacking viscin threads; ovary inferior; style filiform, included or exerted, glabrous; stigma truncate or punctiform. **Fruit** a berry; seeds numerous.

*Gonocalyx* is a small genus of 11 species distributed in Costa Rica, Panama, Colombia, and the West Indies. It is characterized by having pedicels articulate with the calyx; tubular or cylindric corollas; isomorphic stamens with long, thin tubules; and dehiscent by nearly terminal, oblique pores or short slits. Its generic relationships are still uncertain, although Luteyn (1976b) suggested a relationship to *Siphonandra* Klotzsch. Five species are currently known to occur in Costa Rica.

## Key to the Species of *Gonocalyx*

- 1a. Flowers solitary or in pairs; anthers 11–19 mm long ..... 2
- 1b. Flowers in racemes; anthers 7–11 mm long ..... 3
- 2a. Staminal filaments connate; leaf blades ovate to pyriform; pedicels 1–3 (10) mm long; calyx 5–8 (10) mm long ..... *G. almedae*
- 2b. Staminal filaments distinct; leaf blades elliptic to obovate; pedicels 5–9 (13) mm long; calyx 3–4.5 mm long ..... *G. pterocarpus*

- 3a. Rachis 3–7 cm long; bracteoles large, 13–16 mm long, apical; calyx tube conspicuously ribbed at base or narrowly winged; calyx lobes 3–5 mm long ..... *G. megabracteolatus*
- 3b. Rachis 0.9–1.8 cm long; bracteoles small, 1–2 mm long, basal; calyx tube terete or bluntly pentagonal, or base slightly expanded as a rim; calyx lobes 0.3–2 mm long ..... 4
- 4a. Leaves sessile, amplexicaul ..... *G. amplexicaulis*
- 4b. Leaves petiolate, not amplexicaul ..... 5
- 5a. Mature stems, rachis, pedicels, calyx, corollas and fruits glabrous; floral bract ca. 1 mm long; staminal filaments distinct; plants epiphytes ..... *G. costaricensis*
- 5b. Mature stems, rachis, pedicels, calyx, corolla and fruits short-pilose; floral bract 5–20 mm long; staminal filaments connate; plants terrestrial ..... *G. liliae*

**Gonocalyx almedae** Luteyn, Brittonia 28: 403, fig. 1. 1976. Figure 3.

Epiphytic **shrubs** 1–3 m tall; mature stems coarsely and bluntly angled, glabrous, reddish-brown; bark thin, cracking longitudinally; twigs terete to subterete, puberulent, grayish- to reddish-brown; axillary buds awl-shaped, 1.5–3 mm long, appearing stipular. **Leaves** with petioles subterete, 1.5–2.5 mm long, puberulent adaxially; leaf blades coriaceous, ovate, lanceolate to pyriform, 1–3 cm long, 0.5–1 cm wide, base rounded or obtuse, apex obtusely acuminate, margin crenate with each tooth gland tipped, glabrous, obscurely 3–5-plinerved, only midrib prominent. **Inflorescences** axillary, flowers solitary; floral bract ovate, 2–2.5 mm long, apex acuminate, margin glandular-fimbriate; pedicels 1–3 mm long (in one case 10 mm), glabrous or puberulent; bracteoles basal, concealing pedicel, ovate, 1–2.5 mm long, apex acuminate, margin glandular-fimbriate. **Flowers** 5-merous with calyx puberulent or glabrous, 5–8 (10) mm long, 5-winged, tube 2.5–5 mm long, limb erect-patent, sometimes striate, 2.5–4 mm long, lobes long-triangular, acute, 1.5–2 mm long, sinuses rounded to broadly obtuse; **corolla** thin-carnose when fresh, bistratose, cylindric, 21–26 mm long, 2.5–4.5 mm diam., glabrous or puberulent externally but pilose at throat and lobes internally, also bearing scattered glandular fimbriae, bright red, lobes triangular 1–2 mm long; **stamens** 22–24 mm long, sometimes apparently alternately unequal; filaments connate into a tube 5–6.5 mm long, glabrous; anthers 18–19 mm long, thecae 3.5–4 mm long, tubules ca. 13–15 mm long, dehiscing by oblique pores ca. 0.5 mm long; style exserted, 24–27 mm long. **Berry** not seen.

*Gonocalyx almedae* is found in premontane cloud forest, 1000–1600 m elevation. It is distributed in Costa Rica (Cordillera de Talamanca) and western Panama (Chiriquí Prov.) and is infrequently collected (ca. six collections). Flowering specimens have been collected in March, October, and December; fruits are unknown. **Endangered.**

*Gonocalyx almedae* is characterized by having ovate, lanceolate, to pear-shaped leaf blades; solitary, pentamerous flowers; tiny bracteoles; and connate staminal filaments. It is reminiscent of and probably most closely related to *G. pterocarpus* but is distinguished from the latter by its leaf

shape; shorter pedicels; longer, puberulent calyx and corolla; connate filaments; and poroid anther dehiscence.

**Gonocalyx amplexicaulis** Luteyn, Syst. Bot. 15: 745, fig. 1. 1990.

Epiphytic **shrubs**, somewhat scandent; mature stems terete, weakly striate, glabrous, nitid; twigs terete, glabrous. **Leaves** sessile, strongly amplexicaul; leaf blades subcoriaceous, broadly ovate to subrotund, 7–8.5 cm long, 4.6–6.5 cm wide, base rounded, strongly and deeply cordate with lobes overlapping, apex sharply acuminate, margin thin, scarious and minutely toothed in apical half, glabrous but both surfaces bearing minute, deciduous, glandular fimbriae ca. 0.3 mm long, plinerved with 11–13 nerves arising from near base, arcuate and anastomosing near margin, midrib and lateral nerves plane to slightly raised on both surfaces, reticulate veinlets obscure and  $\pm$  plane. **Inflorescences** racemose, 3–4-flowered; rachis subterete, weakly striate, 0.9–1.7 cm long, glabrous; floral bract persistent, ovate, 1–1.8 mm long, apex acuminate, margin glandular-fimbriate; pedicels subterete, striate becoming ribbed apically, 16–20 mm long, glabrous but bearing scattered, glandular fimbriae ca. 0.3 mm long apically; bracteoles persistent, nearly basal, ovate, 1–1.2 mm long, acuminate, margin glandular-fimbriate. **Flowers** (not fully mature) 5-merous; calyx 4.5–5 mm long, glabrous, tube cylindric-campanulate, strongly but bluntly angled opposite sinuses, 2.5–3 mm long, limb campanulate, 2–2.3 mm long, lobes bluntly apiculate, 0.3–0.5 mm long, sinuses concave; **corolla** carnose, bistratose, apparently globose-urceolate, ca. 11 mm long, glabrous but bearing scattered, glandular fimbriae throughout, orange (fide label), lobes bluntly triangular or deltate, ca. 1.5 mm long; **stamens** equal, ca. 8–9.5 mm long; filaments ca. 1.4 mm long, glabrous; anthers 8–9 mm long, thecae ca. 3 mm long, incurved at base, tubules ca. 6 mm long, dehiscing by tiny, oblique, terminal pores; style included, ca. 5 mm long. **Berry** not seen.

*Gonocalyx amplexicaulis* is known only from the type collection, from Continental Divide premontane cloud forest at the Fortuna Dam site, Chiriquí Province, Panama, 1200–1400 m elevation. It has not yet been collected in Costa Rica. The type collection was flowering in June, but the

flowers are immature; fruits are unknown. **Endangered.**

*Gonocalyx amplexicaulis* is a very distinct species easily recognizable by its strongly amplexicaul leaves with sharply acuminate blade apices. Its lianoid habit, leaf size, calyx shape, corolla size, and type of anther dehiscence are similar to those of *G. smilacifolius* (Grisebach) A. C. Smith. That species is limited to the Caribbean islands of Dominica and Guadeloupe, however, and furthermore has petiolate, ovate to ovate-lanceolate leaf blades, longer pedicels, more flowers per inflorescence, and smaller corollas. Nevertheless, morphologically, *G. amplexicaulis* and *G. smilacifolius* are similar and may be each other's closest relatives. Additional material is needed, especially with mature flowers.

***Gonocalyx costaricensis*** Luteyn, Brittonia 28: 40, fig. 2. 1976. Figure 4.

Epiphytic **shrubs**, without lignotuber; mature stems terete, striate, glabrous, reddish; bark thin, cracking in a reticulate pattern, reddish; twigs terete to subterete, often flattened with blunt angles, smooth to minutely striate, glabrous, reddish-brown. **Leaves** with petioles subterete, flattened adaxially, rugose, ca. 2 mm long and 1 mm diam., glabrous or puberulent; leaf blades coriaceous, ovate-lanceolate or elliptic-lanceolate, 2.5–6 cm long, 1–1.5 cm wide, base rounded or obtuse, apex long-acuminate, tip ultimately blunt, glabrous, obscurely 3 (5)-plinerved, midrib and lateral nerves plane to slightly raised on both surfaces, reticulate veinlets raised slightly on both sides but conspicuous only beneath. **Inflorescences** axillary, solitary, racemose, 8–16-flowered; rachis subterete, smooth, glabrous, 1–1.8 cm long; floral bract persistent, linear-lanceolate or aristate, ca. 1 mm long, ca. 0.5 mm wide, glandular-fimbriate at base, ciliate apically; pedicels gradually thickening apically, striate, glabrous, 4–10 mm long and 0.5–1 mm diam., sometimes with cartilaginous teeth apically; bracteoles basal, aristate, ca. 1 mm long, ciliate apically. **Flowers** with calyx glabrous, 6–9.5 mm long, tube cylindric or obconic and spreading apically, slightly expanded as a rim at base but not conspicuously apophysate, conspicuously striate, 1.5–4.5 mm long, limb cylindric-spreading, conspicuously striate, 4.5–5 mm long, lobes broadly triangular, acute, striate, 1–2 mm long, sinuses obtuse; **corolla** thinly carnose, bistratose, cylindric, 12–18 mm long, 5–7 mm diam., glabrous, red, lobes triangular, 1.2–1.5 mm long, obtuse to acute; **stamens** equal, 11–13.5 mm long; filaments distinct at anthesis, marginally pilose, 2–4.3 mm long; anthers 9.5–14 mm long, thecae 2–3.5 mm long, the base short-apiculate, tubules ca. 7–11 mm long, dehiscing by oval, subterminal pores, 0.5–1.6 mm long; style strongly exerted, 14–19 mm long. **Berry** (only one seen) spherical, to 10 mm diam., striate.

*Gonocalyx costaricensis* is endemic to the low-montane, wet forest region around Monteverde,

Costa Rica (Cordillera de Tilarán), 1100–1600 m elevation. It is known only from that area and from only 20 collections. Flowering specimens have been collected in February–April, June, and October–December; fruiting in May. **Endangered.**

*Gonocalyx costaricensis* is characterized by its flowers in racemes; tiny, aristate, basal bracteoles; terete and conspicuously striate calyx; red corolla, which is 12–18 mm long; and distinct staminal filaments. It is morphologically similar to *G. liliae* but is distinguished by glabrous or glabrate (not short-pilose) vegetative and floral parts, shorter floral bracts (1 mm vs. 5–20 mm long), and distinct (not connate) staminal filaments. At Monteverde, *G. costaricensis* may be easily confused with *Vaccinium monteverdense*, which grows in the same general area and has a similar epiphytic habit, leaves, striate calyx limb, and rather broad corolla. *Gonocalyx costaricensis*, however, normally has flat (not somewhat concave) leaves, totally red corollas that are strictly cylindric and much thinner in texture (vs. corollas greenish but suffused with red or purple, broadly cylindric-campanulate in shape and subcarinose), and stamens with thin, erect, elongated tubules (vs. tubules wide, spreading, and shorter with respect to thecae) (see Luteyn, 2001: 444). The species is visited by hummingbirds (pers. observ.).

***Gonocalyx liliae*** Al. Rodr. & J. F. Morales, Novon, in prep. (Hollowell, pers. comm.), fig. 1. 2004. Figure 5.

Terrestrial **herbs** (fide label) 30–50 cm tall, erect or pendent; mature stems glabrate, lightly striate; twigs reddish-brown to grayish-brown, short-pilose. **Leaves** alternate to rarely subopposite, with petioles 2–4 mm long; leaf blades coriaceous to subcoriaceous, ovate to narrowly ovate, slightly revolute, 1.9–4 cm long, 0.8–2 cm wide, base obtuse, apex acute, margin entire, sparsely pilose on both surfaces, the lower usually glandular fimbriate, obscurely plinerved. **Inflorescences** axillary, terminal or subterminal, solitary, racemose, 4–6-flowered; rachis subterete, slightly ribbed, pilose, 1–1.5 cm long; floral bract persistent, foliaceous, ovate, 5–20 mm long, apex acute; pedicels subterete, striate, 8–11 mm long, pilose; bracteoles deciduous, basal, linear, 0.4–0.8 mm long. **Flowers** with calyx ca. 10 mm long, short-pilose, tube campanulate, terete, 4–5 mm long, ca. 4 mm diam., limb campanulate, suberect, 4–5.5 mm long, lobes 1–1.2 mm long, deltate, acute; **corolla** campanulate, tube ca. 12 mm long, ca. 3 mm diam., reddish to orangish-red, pilose, lobes deltate, acute, 2–2.5 mm long; **stamens** equal, slightly shorter than corolla; filaments connate, 2–2.5 mm long, sparsely pilose; anthers ca. 9.5 mm long, thecae incurved at base, ca. 2.3 mm long, tubules ca. 7 mm long, dehiscing by terminal,

oblique and introrse pores; style ca. 6 mm long. **Berry** immature, subglobose, shortly pilose, greenish-red.

*Gonocalyx liliae* is endemic to Costa Rica, where it is found in the pluvial oak forest of the Pacific slopes in the Cordillera de Talamanca, 1600–2000 m. The only known collections are San José: Cantón de Acosta, Fila Bustamante, Hacienda Tiquires, cabeceras Río Tiquires, J. F. Morales 4279; Cantón de Dota, Providencia, A. Rodríguez 7261, and “Santa Rosa de Copey,” Tonduz 12237. Flowering collections have been made in April–May; fruiting between May and June. **Endangered.**

Among the Costa Rican species of *Gonocalyx*, *G. liliae* is easily recognized by its conspicuous pubescence of its vegetative, floral, and fruiting parts; flowers in racemes; terete calyx tube; and connate staminal filaments. It shares similar vegetative and inflorescence features with *G. costaricensis*, but the latter has glabrous parts, inconspicuous floral bracts, and distinct staminal filaments. [The above description and discussion are based on the protologue; the authors have not yet seen the type collection, and the Tonduz collection lacks corollas and stamens.]

***Gonocalyx megabracteolatus*** (Wilbur & Luteyn) Luteyn, Brittonia 53: 437. 2001. *Macleania megabracteolata* Wilbur & Luteyn, Ann. Missouri Bot. Gard. 68: 163. 1981.

Epiphytic **shrubs**, without lignotuber; mature stems and twigs subterete, conspicuously and bluntly to narrowly ridged and grooved, striate, glabrous or nearly so, scattered glandular-fimbriate, the basal portion of each year's growth conspicuously surrounded by a series of persistent, tightly clasping, imbricate, ovate to elliptic, acute to rounded, striate, glabrous perulae 5–20 mm long. **Leaves** with petioles stout, rugose, 3–6 mm long, densely short-pilose, or puberulous to glabrate; leaf blades coriaceous, elliptic, slightly revolute, (5) 7–10 (12.5) cm long, (2.7) 3–4 (5.7) cm wide, base rounded or broadly tapering, apex acute or more typically acuminate with the tip 1 cm or more long, margin entire, glabrous above or sparingly to moderately spreading short-pilose or puberulent along basal raised portion of midrib, glabrate beneath, younger leaves with reddish-brown appressed, glandular fimbriae 0.1–0.2 mm long that leave punctate depressions when deciduous, 5–7-plinerved with lateral veins arising at or near base, midrib much thickened and prominently raised in basal 1 cm then becoming impressed apically, raised beneath, lateral nerves slightly raised basally then impressed apically above and slightly raised beneath, reticulate veinlets obscure above and slightly raised but obscure beneath. **Inflorescences** axillary, borne near ends of branches, sessile, racemose, 4–7-flowered, all parts weakly to moderately reddish-brown appressed glandu-

lar-fimbriate with fimbriae 0.1–0.2 mm long; rachis striate or irregularly angled, 3–7 cm long, lower 1.5–2 cm enveloped by persistent, ovate to oblong bracts (inflorescence), 5–8 mm long; floral bract oblong to spatulate, 9–13 mm long, apex rounded, margin entire; pedicels striate, 5–11 mm long, apically broadened; bracteoles apical or up to 10 mm below apex, elliptic, striate, 13–16 mm long, ca. 5 mm wide, apex acute. **Flowers** with the calyx 10–12.5 mm long, moderately to densely glandular-fimbriate with reddish-brown fimbriae, tube  $\pm$  pentagonal, strongly ribbed at base or narrowly winged in lower half continuing apically onto limb, 4–6 mm long, limb striate, campanulate-spreading, 6–8 mm long, lobes striate, deltate, 3–5 mm long, apex acute, sinuses acute; **corolla** thinly carmose, unistratose, broadly cylindric-campanulate, terete, 12–18 mm long, 7–16 mm apical diam., glabrous but scattered glandular-fimbriate, pale greenish but suffused with red on surfaces exposed to sun, lobes broadly triangular-deltoid, acute, 2–3 mm long; **stamens** 10, ca. 10–13.5 mm long; filaments distinct, 3–5 mm long, spreading long-pilose with slender trichomes 0.2–0.4 mm long; connectives smooth; anthers (7) 8–10 mm long, curving slightly inward, thecae 3–3.5 mm long, the base incurved and shortly and bluntly apiculate, tubules 2, (3.5) 5–6.5 mm long, dehiscing by apically oblique, oval clefts ca. 0.8–1 mm long; style 18–19 mm long, glabrous,  $\pm$  sigmoid. **Berry** not seen.

*Gonocalyx megabracteolatus* is found in premontane cloud forest, 1100–2050 m elevation. It is endemic to western Panama (several collections from Chiriquí Prov.) and eastern Costa Rica (one collection, San José: Cantón de Coto Brus, Zona Protectora Las Tablas, Cuanca Térraba-Sierpe, Surá, 7 km NW of Progreso, Navarro V. & Picado 583). Flowering material has been collected in January, February, April, and October; fruits are unknown. **Endangered.**

*Gonocalyx megabracteolatus* is characterized by having flowers in racemes, large bracteoles borne at the apex of the pedicel, broadly cylindric-campanulate corolla, and distinct staminal filaments. It was first described in the genus *Macleania* by Wilbur and Luteyn (1981), but its relationships were obscure at that time. After a detailed examination of the stamens from all known material of this taxon, it was transferred to *Gonocalyx*, the morphological placement being reinforced by molecular data (cf. Luteyn, 2002). That study showed the taxon fell into the same clade and is a sister species of *G. costaricensis*. We do not, however, feel that *G. megabracteolatus* is closely related to *G. costaricensis* at the species level and await a more detailed morphological study of *Gonocalyx* to decide its placement.

***Gonocalyx pterocarpus*** (J. D. Smith) Luteyn, Brittonia 28: 38, fig. 1. 1976. *Themistoclesia pterocarpa* J. D. Smith, Bot. Gaz. 44: 113.



1907. *Cavendishia pterocarpa* (J. D. Smith) A. C. Smith, Contrib. U.S. Natl. Herb. 28: 449. 1932. Figures 2O, 3, and 7.

Epiphytic **shrubs** or sometimes small, stunted trees in elfin forest with branches 3–6 m and bole to 20 cm diam.; mature stems terete to subterete, short puberulent or glabrate, striate, reddish- to blackish-brown; bark thin, cracking longitudinally twigs subterete, bluntly angled, densely puberulent. **Leaves** with petioles subterete, channeled adaxially, somewhat winged, 1–3 mm long, densely short puberulent; leaf blades coriaceous, obovate, oblong-elliptic or elliptic, 1–2 (3) cm long, 0.5–1.5 cm wide, base cuneate and attenuate, apex rounded and slightly emarginate, margin entire or remotely crenate apically, scattered hairs on midrib adaxially, obscurely 5-plinerved, all nerves slightly raised on both surfaces. **Inflorescences** axillary, 1–2-flowered, subtended by 3–5, ovate, acute, ciliate and fimbriate margined bracts, 0.7–1.5 mm long, 0.5–1 mm wide, not clearly differentiated into inflorescence bracts, floral bracts, or bracteoles; pedicels subterete to bluntly angled, slightly thickening and oblique apically, 5–9 (13) mm long, ca. 1 mm diam., glabrous, with few cartilaginous teeth apically. **Flowers** with calyx glabrous, 3–4.5 mm long, obprismatic, 5-winged opposite sinuses, tube 1.5–2.5 mm long, limb campanulate, 1.5–2 mm long, lobes triangular, acute, ca. 0.5 mm long, sinuses rounded to flat; **corolla** thinly carnose when fresh and membranous, bistratose, cylindric, narrowed to throat, slightly pentagonal, (14) 16–20 (25) mm long, 3–6 mm diam., glabrous externally but with scattered, short, glandular-fimbriae, crimson when fresh, lobes triangular or oblong, to 3 mm long, apex obtuse, throat and lobes densely white pubescent internally; **stamens** equal, 14–19 mm long; filaments distinct, 3–5 mm long, glabrous, white; anthers 11–16.5 mm long, thecae 2.5–4 mm long, tubules ca. 8.2 mm long, dehiscing by lateral slits 3.5–4 mm long; style 19–23 mm long, sometimes exserted. **Berry** spherical, 8–10 mm diam., dark blue-black.

*Gonocalyx pterocarpus* is found in premontane cloud forest, 1000–2400 m elevation. It is distributed in Costa Rica (Cordillera Tilarán and Cordillera Central) and western Panama (Chiriquí Prov.). Flowering occurs throughout year; fruiting collections have been made in January, April, June, July, November, and December. **Rare/Infrequent.**

*Gonocalyx pterocarpus* is characterized by its 1–2-flowered inflorescences, obprismatic calyx tube that is narrowly 5-winged to the sinuses, distinct staminal filaments, anther tubules 3–4 times longer than the thecae and dehiscing by lateral slits, and internally densely short-pubescent corolla lobes. It is morphologically similar to and

can superficially be confused with *G. almedae*. *Gonocalyx pterocarpus* differs by having longer pedicels that are glabrous (5–9 [13] mm vs. normally 1–3 mm long, glabrous or puberulent), a shorter calyx (3–4.5 mm not 5–8 [10] mm long), and distinct staminal filaments (not connate). The species is visited by the hummingbird *Lampornis calolaema* in Costa Rica (pers. observ.; Luteyn, 1998).

## Lateropora A. C. Smith

REFERENCES—R. L. Wilbur & J. L. Luteyn, Additions to the Ericaceae of Panama. Ann. Missouri Bot. Gard. 68: 162–163. 1981. J. L. Luteyn, New species, new records, and neotypification of some Mesoamerican Ericaceae. Brittonia 48: 241–249. 1996 [*Lateropora*, pp. 246–247].

Terrestrial or epiphytic **shrubs**. **Leaves** alternate, petiolate, the blade coriaceous, the margin entire, the venation plinerved. **Inflorescences** axillary, compact, umbelliform or racemose; floral bract persistent; pedicels articulate with calyx, short, stout; bracteoles 2, basal, subopposite, persistent. **Flowers** 5-merous, without odor; calyx synsepalous, tube campanulate, lobes erect; **corolla** sympetalous, aestivation valvate, thick-carnose, bistratose, broadly urceolate or shortly campanulate, densely pilose internally; **stamens** 10, equal, nearly as long as the corolla; filaments distinct, weakly adnate to base of corolla; connectives lacking disintegration tissue or spurs; anthers lacking awns, thecae strongly papillate, tubules 2, distinct, short (vestigial), dehiscing laterally by clefts extending entire length of anther; pollen grains in tetrahedral tetrads, lacking viscin threads; ovary inferior; style filiform, glabrous. **Fruit** a berry; seeds numerous.

*Lateropora* consists of three species distributed from eastern Costa Rica to central Panama. The genus is characterized by succulent, dark green corollas and anthers with vestigial to short tubules dehiscing laterally along the entire length of the anther. The genus is unique in its type of anther dehiscence and is in a rather isolated position within the Vaccinieae, although its overall relationships may lie with the green-flowered species of *Vaccinium* (e.g., *V. poasanum*, *V. costaricense*, etc.). One species is currently known to occur in Costa Rica.



## Key to the Species of *Lateropora*

- 1a. Calyx lobes 2–3 mm long, 4–5 mm wide basally; corolla lobes ca. 3 mm long; petioles 5–15 mm long; leaves 6–13 cm long, 4–9 cm wide . . . . . *L. ovata*  
1b. Calyx lobes 1–1.5 mm long, 1.8–2.2 mm wide basally; corolla lobes 1–2 mm long; petioles 3–4 mm long; leaves 2.5–3.8 cm long, 1.2–1.8 cm wide . . . . . *L. tubulifera*

***Lateropora ovata*** A. C. Smith, Contrib. U.S. Natl. Herb. 28: 334. 1932. *Symphysia ovata* (A. C. Smith) vander Kloet, Taxon 53: 97. 2004. Illustration: A. C. Smith, Contrib. U.S. Natl. Herb. 28: pl. 1. 1932. R. L. Wilbur & J. L. Luteyn, Ann. Missouri Bot. Gard. 65: 91, fig. 9. 1978. Figures 2J and 10.

Epiphytic or terrestrial **shrubs** 2–3 m tall; mature stems and twigs subterete, glabrous, striate, thick and widely divergent. **Leaves** with petioles rugose, 5–15 mm long, 1.5–3 mm diam., narrowly winged apically, glabrous; leaf blades thick-coriaceous, ovate to broadly elliptic, sometimes nearly orbicular, 6–13 cm long, 4–6 (9) cm wide, base cuneate, apex acute to broadly obtuse, bluntly short-acuminate or nearly rounded, glabrate but with appressed, reddish-brown, glandular-fimbriae 0.2–0.6 mm long, 3–5 (7)-plinerved with inner pair of lateral veins arcuate, arising above base and sometimes subopposite, midrib thickened and raised in basal  $\frac{1}{3}$ – $\frac{1}{4}$  then apically impressed above, raised and conspicuous beneath, inner 1–2 pairs of lateral nerves impressed above and raised beneath, usually conspicuous but sometimes inconspicuous beneath, the outer pair of lateral nerves sometimes raised above but always obscure, reticulate veinlets slightly elevated but often obscure on both surfaces. **Inflorescences** axillary, compact umbelliform racemes; rachis stout, 12–16 mm long, glabrous, bracteate at base; floral bract thick, scale-like, broadly ovate, 4–5 mm long, 3.5–4.5 mm wide, apex rounded, margin ciliate and glandular-fimbriate; pedicels 3–10 mm long, ca. 2 mm in diam., glandular-fimbriate with trichomes 0.1–0.2 mm long at apex; bracteoles 2, basal to submedial, subopposite, keeled, broadly ovate, 3–4 mm long, 4–5 mm wide, apex rounded, ciliate. **Flowers** with calyx ca. 6 mm long, sparingly appressed glandular-fimbriate, tube cylindric-campanulate, usually pentagonal and bluntly 5-ribbed opposite sinuses, 3.5–5 mm long, ca. 4 mm diam., limb thick-walled, campanulate, 1–2.5 mm long, glabrous, lobes broadly triangular, acute, 2–3 mm long, 4–5 mm wide at base, erect or incurved, short-ciliate, sinuses concave at anthesis or sometimes tearing and then acute; **corolla** broadly urceolate or subglobose, 6–8 mm long, 7–8 mm diam., pale greenish-white, sparsely pubescent externally near middle with appressed trichomes 0.4–0.6 mm long, lobes triangular, ca. 3 mm long, 4.5–5 mm wide at base, acute, spreading to reflexed, densely tangled villous internally with white trichomes 0.4–0.7 mm long; **stamens** 10, ca. 6.7–7 mm long; filaments 3–4 mm long, broadened at base to ca. 1 mm wide, tapering gradually upward to ca. 0.6 mm, glabrous in basal  $\frac{1}{3}$ , strikingly pilose apically especially near connective with trichomes 0.5–1 mm long; anthers 3–5 mm long, thecae ca. 2.7–4 mm long, strongly in-

curved at base with lower  $\frac{1}{3}$  protruding inwardly or even turning upward, tubules submembranous, ca. 0.3–0.7 mm long; style stout, ca. 7 mm long. **Berry** not seen.

*Lateropora ovata* is found in premontane cloud forest, 1100–2200 m elevation. This little-known species has been collected only from western Chiriquí Province, Panama (nine collections) and once in the eastern Cordillera de Talamanca, Costa Rica (Limón Prov., Cantón Talamanca, Dto. Bratsi, Reserva Indígena Bri Bri, 1.7 km SW of Kivut and 6.1 km SW of Alto Lari, Schmidt 642). Flowering specimens have been collected in January, February, and March; fruits are unknown.

### Endangered.

*Lateropora ovata* is characterized by its coriaceous, large, ovate to broadly elliptic, basally cuneate leaves and compact umbelliform racemes. It may be distinguished from the other two species in the genus by its combination of larger and coarser leaves with longer petioles and longer calyx and corolla lobes (a key to the three species is provided in Wilbur & Luteyn, 1981). More collections are needed to understand the range of variation in this and all species of *Lateropora* and to determine their interspecific relationships.

***Lateropora tubulifera*** Wilbur & Luteyn, Ann. Missouri Bot. Gard. 68: 162. 1981. *Symphysia tubulifera* (Wilbur & Luteyn) vander Kloet, Taxon 53: 97. 2004.

**Shrubs** 1.5 m tall, with twigs moderately thick, striate to irregularly angulate, 2–2.5 mm diam., glabrous. **Leaves** with petioles flattened adaxially, 3–4 mm long, 2–2.5 mm wide, glabrous; leaf blades coriaceous, elliptic, 2.5–3.8 cm long, 1.2–1.8 cm wide, base acutely tapering, apex acute to obtuse, margin slightly thickened, glabrous or glabrate beneath, 5-plinerved with inner pair of lateral nerves arising from basal 2 cm, midrib conspicuously thickened and raised in proximal 1–2 cm then impressed apically above and conspicuously raised beneath, lateral nerves impressed completely or only basally above and conspicuously raised beneath, reticulate nerves slightly impressed, plane or slightly raised above, sometimes obscure, raised beneath. **Inflorescences** corymbosely racemose, (1) 3–5-flowered, 2–3 cm long overall, circumscribed at base by 3–4, broadly oblong to orbicular, short-ciliate bracts, 1–3 mm long, ca. 1.5–2.2 mm wide; rachis 1–1.5 cm long, glabrous; floral

bract ovate to oblong, 1.5–2.5 mm long, 1.5–2 mm wide, slightly keeled and short-apiculate, irregularly narrowly hyaline margined, glabrous, short-ciliate; pedicels slightly clavate, 10–18 mm long, medially ca. 1 mm diam., glabrous except for inconspicuous fringe of glandular fimbriae borne apically at articulation with trichomes 0.2–0.4 mm long; bracteoles located along basal  $\frac{1}{3}$  of pedicel, appressed, subopposite to alternate, ovate to oblong, 2–2.6 mm long, 1.5–1.8 mm wide, ciliate, irregularly hyaline margined. **Flowers** with calyx 3–6 mm long, 3–3.2 mm diam., glabrous, tube campanulate, ca. 2.5 mm long, bluntly 10-ribbed in lower  $\frac{1}{2}$ , limb somewhat flaring or at least wider than tube, ca. 2.5–3.5 mm long, lobes erect, deltate, 1–1.5 mm long, 1.8–2.2 mm wide at base, apex acute; **corolla** urceolate, 3.5–7 mm long, to 7 mm diam., externally glabrous but internally densely pilose to tangled villous in apical  $\frac{1}{2}$  with white trichomes 0.6–1 mm long, pink (fide label), lobes triangular, 1–2 mm long, acute, glabrous externally and densely tangled villous internally; **stamens** ca. 5.2 mm long; filaments 2–2.5 mm long, <0.5 mm wide at base, densely pilose apically with white trichomes 0.5–1.2 mm long; anthers conspicuously granular, 2.5–4.2 mm long, thecae strongly incurved in basal  $\frac{1}{4}$ – $\frac{1}{3}$ , tubules 0.8–1.2 mm long. **Berry** not seen.

*Lateropora tubulifera* is known from only three collections, from short, windswept, montane cloud forest in the Fortuna Dam region, Chiriquí Province, Panama, 1800–2120 m elevation. The species has not yet been collected in Costa Rica. Flowering specimens have been collected in January, February, and May; fruits are unknown. **Endangered.**

*Lateropora tubulifera* is characterized by its anther tubules, at least twice as long as those of the other two species, and its small leaf blades.

## Macleania W. J. Hooker

REFERENCES—P. Yeo, Notes on some species of *Macleania* (Ericaceae). *Baileya* 15: 45–59. 1967. J. L. Luteyn, A review of and taxonomic realignments within the neotropical genus *Macleania*

(Ericaceae: Vaccinieae). *BioLlania* 6: 455–465. 1997.

Epiphytic or terrestrial **shrubs** sometimes arising from lignotubers. **Leaves** alternate, petiolate, the blade coriaceous, the margin entire, the venation pinnate or plinnerved. **Inflorescences** axillary (in ours) or terminal, racemose or subfasciculate, few- to many-flowered, rarely flowers solitary; pedicels articulate with calyx (in ours) but this sometimes obscure or rarely continuous; bracteoles basal to medial. **Flowers** 5-merous, without odor; calyx synsepalous, tube short-cylindric or campanulate, often angled to conspicuously winged, the wings sometimes protruding beyond calyx limb as spurs (not ours), limb erect, spreading; **corolla** sympetalous, aestivation valvate, subcylindric or elongate urceolate; **stamens** 10, equal, about  $\frac{1}{4}$  to nearly equaling corolla in overall length; filaments distinct or connate, abaxially attached to anthers near their bases; connectives lacking disintegration tissue or spurs; anthers stout, lacking awns, thecae conspicuously papillate, tubules about as long as thecae, 1 or 2 (then laterally connate but with a septum present, or distinct, rarely completely distinct), rigid, broadly conical, dehiscing by introrse, elongate, distinct or fused clefts; pollen grains in tetrahedral tetrads, lacking viscin threads; ovary inferior; style filiform, exerted; stigma truncate. **Fruit** a berry; seeds numerous, often with a mucilaginous sheath, the embryo sometimes green.

*Macleania* consists of approximately 38 species distributed from Mexico to Peru. The genus is characterized by stamens of equal lengths but  $\frac{1}{4}$ – $\frac{2}{3}$  as long as the corolla; staminal connectives without spurs; anther tubules often short, elongate-conical, rigid, and only laterally to totally fused; and ovary inferior. The genus has been divided into two very distinct subgenera, each with one species in Costa Rica (Luteyn, 1997). *Macleania* is related to *Psammisia*, differing most conspicuously by its staminal connectives that lack spurs (vs. spurs present or absent in *Psammisia*) and anther tubules connate (not distinct to the base). Two species are currently known to occur in Costa Rica. The genus is currently being revised by J.L.L.

## Key to the Species of *Macleania*

- 1a. Anther tubules 1; staminal filaments connate (rarely distinct); calyx sharply angled to winged; corolla angled, totally orange, densely white pilose at throat and lobes internally; berry translucent white (subgen. *Macleania*) ..... *M. insignis*
- 1b. Anther tubules 2; staminal filaments distinct; calyx essentially terete or pentagonal; corolla terete or pentagonal, reddish with white or pinkish throat, glabrous internally; calyx and corolla essentially glabrous; berry blue-black (subgen. *Aponema*) ..... *M. rupestris*

***Macleania insignis*** M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 9: 531. 1842. *Thibaudia laurifolia* M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 9: 530. 1842. *M. ovata* Klotzsch, Linnaea 23: 20. 1851. *M. cordata* var. *linearifolia* J. D. Smith, Bot. Gaz. 16: 12. 1891. *M. linearifolia* (J. D. Smith) A. C. Smith, Contrib. U.S. Natl. Herb. 28: 368. 1932. *M. insignis* var. *linearifolia* (J. D. Smith) Standl. & L. O. Williams, Fieldiana, Bot. 31: 172. 1965. *M. subracemosa* L. O. Williams, Fieldiana, Bot. 31: 172. 1965. Figures 2L, 6, and 7.

Epiphytic or terrestrial, infrequently epipetric **shrubs** 0.5–2 (4) m tall, arising from a lignotuber; mature stems terete, glabrous to pilose, glabrate, often nitid, light to dark brown; bark exfoliating in thin sheetlets, reddish-brown; twigs bluntly angled, glabrous to often densely short-puberulous with white hairs. **Leaves** with petioles terete or subterete then flattened adaxially, rugose, (1) 2–4 (6) mm long, glabrous or rarely densely short-puberulous; leaf blades ovate to lance-ovate, elliptic to elliptic-ovate, rarely lance-oblong, oblong or suborbicular, (2) 3–8 (12) cm long, (1) 1.5–4 (5.6) cm wide, base rounded, usually subcordate, apex obtuse to acute, glabrous on both surfaces but usually with brownish, glandular fimbriae especially beneath, lower surface also often with a dark, circular, concave gland ca. 0.2 mm diam. on either side of midrib base, pinnately nerved with 3–4 secondary nerves per side, or 3–5 (7)-plinerved with lateral nerves originating near base, midrib thickened in basal 0.6–3.5 cm and slightly impressed above and raised beneath or more usually slightly raised on both surfaces, lateral nerves and veinlets usually slightly raised on both surfaces. **Inflorescences** axillary, sessile, subfasciculate to rarely short-racemose, (1) 2–3 (5)-flowered; rachis (when present) subterete, rugose, 0.6–1 cm long, ca. 1.5–2 mm diam.; floral bract persistent, carinate, ovate to triangular-ovate, 1.2–2 mm long, apex short-acuminate, margin ciliate; pedicels subterete, rugose, (4) 8–16 mm long, glabrous or weakly to moderately densely short-pilose, usually also with a few glandular fimbriae apically; bracteoles basal to medial, triangular, 1–3 mm long, with 1–2 circular, dark glands ca. 0.2 mm diam. abaxially at base (the bracteole base sometimes appearing simply darker and thicker in color), often minutely ciliate. **Flowers** with calyx 5.3–8 (10) mm long, glabrous or weakly to moderately densely short-pilose, rarely with a few glandular fimbriae, tube obconic, 3–5 (7) mm long and 3–4 mm diam., glabrous or minutely to moderately appressed short-pubescent, broadly to narrowly but distinctly winged, the wings 0.3–1.8 mm broad, truncate or slightly rounded at base not extended beyond limb apically, limb spreading to erect, 1–3 (4) mm long, conspicuously lobed, lobes narrowly triangular to deltate, (0.4) 0.8–2 mm long, margins rarely ciliate, sinuses flat or acute; **corolla** tubular, slightly expanded at base, contracted at throat, sharply and conspicuously 5-angled, (14) 20–27 (30) mm long, 4–6 (8) mm diam., glabrous to slightly puberulous especially apically externally, throat sparsely to densely villous internally, orange to reddish-orange or rarely pinkish, lobes acute, spreading, 1.5–3 mm long, rarely

greenish; **stamens** 8–13 mm long; filaments connate (rarely distinct) into a tube 3–6 (7) mm long, glabrous; connectives often alternately apically thickened and shouldered; anthers 7–10 mm long, thecae 4–6.5 mm long, tubule 1, 2–4 mm long, dehiscent by a broad introrse cleft more than half the tubule length; style 22–31 mm long, exerted 1–2 mm. **Berry** terete, translucent white, 9–12 mm diam., glabrous.

*Macleania insignis* is found in premontane cloud forest, (650) 900–2400 m elevation. It is distributed from Mexico to Costa Rica. In Costa Rica it is found in the Cordillera Tilarán and western Cordillera Central. Flowering specimens have been collected January–March; fruiting in May. **Locally Common.**

*Macleania insignis* is characterized by its small, ovate to elliptic-ovate leaf blades; few-flowered fasciculate inflorescences; and concolorous corollas. It is the only member of subgen. *Macleania* found in Costa Rica (see Luteyn, 1997). Plants of some populations, mostly in Nicaragua, in the heavily collected area between Jinotega and Matagalpa, have short-racemose inflorescences that may also be pubescent to some degree (= *M. subracemosa*). Frequently these plants may also have staminal filaments that are distinct or only slightly connate. These features are not consistent, however, nor are they correlated in any way; each may be found scattered throughout the Mesoamerican range and may even vary on the same plant. Therefore, we have chosen not to recognize formally any other taxon in this group. A. C. Smith (1932) recognized some populations from southern Central America (as *M. ovata*) that were generally differentiated from the more northern *M. insignis* by longer and broader, deltoid calyx lobes that formed acute basal sinuses with the adjacent lobes. Furthermore, according to Smith, *M. insignis* was considered to have apiculate calyx lobes less than 1.5 mm long that formed a broad, flat sinus between adjacent lobes. There is, however, much greater variability in calyx lobes than was apparent in the relatively few specimens available to Smith, and there is an apparent continuum between the extremes. Hence, there is no way to recognize two taxa based on differences in calyx lobes. Yeo (1967) suggested that *M. ovata* might be best regarded as a geographical subspecies of *M. insignis*, but he did not make the combination, and we see no reason to do so. The calyxine variation does not suggest geographical subspecies since apiculate-lobed plants are found at least as far south as Costa Rica and deltoid, larger-lobed plants are to be found in southern

Mexico along with the apiculate-lobed plants. *Macleania insignis* is morphologically most similar to *M. cordifolia* Benthham from Ecuador; it differs from the other Costa Rican species of *Macleania* by the characters mentioned in the key above. The species is visited by hummingbirds in Costa Rica (pers. observ.).

***Macleania rupestris*** (Kunth in H.B.K.) A. C. Smith, *Phytologia* 1: 131. 1935. *Thibaudia rupestris* Kunth in H.B.K., Nov. gen. sp. pl. 3: 270. 1818. *Psammisia rupestris* (Kunth in H.B.K.) Klotzsch, *Linnaea* 24: 45. 1851. *P. glabra* Klotzsch, *Linnaea* 24: 46. 1851. *P. costaricensis* Klotzsch, *Linnaea* 24: 47. 1851. *M. turrialbana* J. D. Smith, *Bot. Gaz.* 27: 339. 1899. *M. glabra* (Klotzsch) Hoerold, *Bot. Jahrb. Syst.* 42: 268. 1909. *M. costaricensis* (Klotzsch) Hoerold, *Bot. Jahrb. Syst.* 42: 268. 1909. *M. irazuensis* S. F. Blake, *Proc. Biol. Soc. Washington* 35: 121. 1922. *M. racemosa* Cufod., *Arch. Bot. Sist.* 9: 199. 1933. Illustration: R. L. Wilbur & J. L. Luteyn, *Ann. Missouri Bot. Gard.* 65: 100, fig. 11. 1978. Figures 2M and 10.

Epiphytic or terrestrial **shrubs** 0.6–2 m tall, often lianoid, rarely small trees, often with basal lignotubers to 60 cm diam.; mature stems terete to subterete, smooth to furrowed with epidermis cracking longitudinally, dull to nitid, glabrous to rarely moderately puberulent; twigs subterete, bluntly angled, striate, glabrous to densely short-pilose with white hairs to 0.8 mm long. **Leaves** with petioles rugose, sometimes narrowly winged apically, 3–11 (14) mm long, 2–4.5 mm diam., usually glabrous; leaf blades thick-coriaceous, oblong, elliptic, ovate-elliptic to ovate, sometimes spatulate, (2) 4–9.5 (15) cm long, (1.2) 2–5 (7.5) cm wide, base rounded to broadly cuneate, sometimes attenuate, rarely subcordate, apex obtuse or rounded to acute, rarely short-acuminate, usually glabrous but occasionally puberulent or spreading short-pubescent on lower surface near base, occasionally sparsely punctate above, pinnately nerved with 2–4, arcuate-ascending secondary nerves per side, midrib thickened and raised in basal 1–3 cm then slightly impressed apically above and prominently raised beneath, secondary nerves slightly impressed, raised or plane above and prominently raised beneath, reticulate veinlets slightly raised to plane above and slightly raised beneath. **Inflorescences** axillary, racemose, (4) 10–20 (40)-flowered, glabrous throughout or occasionally moderately spreading short-pubescent; rachis subterete, sometimes sharply angled or ribbed, striate, (0.5) 1–3.5 (13) cm long; floral bract deltate or ovate to oblong, 2–5 (7) mm long, 2–3 mm wide, often ciliate, sometimes margin glandular-fimbriate; pedicels subterete, angled, striate, rugose, (7) 10–24 mm long; bracteoles nearly basal to medial, ovate to broadly ovate, broadly deltate to oblong, 1–2 (4) mm long, to 3 mm wide, glabrous or often ciliate, apex acute to rounded or short-acuminate.

**Flowers** with calyx 5–8 mm long, glabrous, tube rugose, short-cylindric, 2.5–4 (5) mm long, terete or bluntly angled, the base truncate, sometimes striate, limb campanulate to spreading, 2–5 mm long, lobes broadly triangular to oblong-ovate, 1–2.5 mm long, apiculate, acute to acuminate, sinuses concave; **corolla** thick-carnose, bistratose, cylindric to somewhat cylindric-urceolate or bottle-shaped, terete or pentagonal, (11) 13–19 (24) mm long, ca. 6–7 mm diam., deep red or pinkish-red at base then paler or yellowish or whitish apically, lobes deltate to oblong, 1.5–3 mm long, usually white, apex acute; **stamens** 9–16 mm long; filaments distinct, 2–5.5 mm long, glabrous or marginally short-pilose; anthers 8–14 mm long, thecae 4–8 mm long, incurved at base, tubules 2 but usually laterally connate to base, rarely distinct, 3–6.2 mm long; style usually long-exserted. **Berry** spherical, glabrous, 12–15 mm diam., dark bluish-black.

*Macleania rupestris* is found in lower montane forest; premontane dry and wet forest; montane moist, wet, and rain forest; subalpine rain forest; and humid páramo, (1400) 2000–3400 m elevation. It is broadly distributed from Costa Rica to Peru. Flowering occurs in nearly every month; fruiting specimens in March–July and September. **Common.**

*Macleania rupestris* is the only member of subgen. *Aponema* in Costa Rica, where it is the third most commonly encountered and collected ericad (following *Cavendishia bracteata* and *Pernettya prostrata*). It is characterized by usually oblong, elliptic, or ovate-elliptic to ovate, sometimes spatulate, pinnately nerved leaf blades; racemose inflorescences; inconspicuous floral bracts; corollas about 2 cm long that are red with white apices; staminal filaments distinct; anther tubules two (but laterally connate); and a dark blue-black berry. The extensive morphological variation in *M. rupestris* is perhaps to be expected in a species as widespread and common as this. Since there are no consistently distinctive populations, we do not consider the variation to be of taxonomic value. Common names include *colmillo*, *muelita*, *muelas*, and *San Juan* (Costa Rica) and *uva* (Panama). In Costa Rica, the hummingbirds *Eugenes fulgens spectabilis* and *Panterpe insignis* forage populations of *M. rupestris* for nectar and probably pollinate it in the process (pers. observ.; Colwell, 1973, as *M. glabra*). The flower-piercer *Diglossa plumbea* also visits *M. rupestris* to rob nectar, which is the reason for the small holes often seen at the base of the corolla. The berry is edible, being sometimes sweet or insipid, and is rarely found in marketplaces; the flowers are said to taste “sour” like *Rumex* (they contain oxalic acid).

## Monotropa Linnaeus

REFERENCES—G. D. Wallace, *Monotropa*. Fl. Neotrop. Monogr. 66: 19–25, 1995.

Fleshy, succulent **herbs** lacking chlorophyll, blackening upon drying, the shoots arising from perennial root masses; mycorrhizal root parasites. **Leaves** reduced to bract-like scales, congested. **Inflorescences** racemose or reduced to a solitary flower (in ours); pedicels recurved; floral bract and bracteoles present but sometimes similar to perianth. **Flowers** (3) 4–5 (6)-merous; calyx similar to corolla, the sepals distinct and imbricate (in ours), or apparently absent; **corolla** cylindrical or campanulate, the petals distinct but imbricate, scale-like, saccate at base, tardily deciduous; **stamens** 8–10 (12); filaments distinct, the outer whorl (opposite petals) shorter than the inner; connectives lacking disintegration tissue or spurs; anthers 1-locular at anthesis, smooth, lacking awns, dehiscent by a single, terminal slit or by ends of a slit which may later open along entire length; pollen grains single, lacking viscin threads; nectaries of 8–10 paired lobes between filament bases; ovary superior, (8) 10-lobed, (4) 5 (6)-locular at base with axile placentation, 1-locular above with 4–5, bilobed parietal placentas; style stout, columnar, thick, fleshy, tapering to ovary; stigma funnel-shaped to discoid, obscurely 4–6-lobed; nectary present as 8–10 lobes projecting from between filament bases. **Fruit** a loculicidal capsule, 4–6-valved, globose to ovoid, 8–10-grooved, erect; seeds numerous, minute, tailed.

*Monotropa* is a genus of two species occurring in circumpolar, boreal, and temperate (= montane in Costa Rica) forests of the United States, Mexico, Mesoamerica, and Colombia. One species occurs in Costa Rica and adjacent western Panama. *Monotropa* is readily characterized by its succulent herbaceous, achlorophyllous, mycorrhizal habit. The genus was placed in its own family, Monotropaceae, until recently but is now considered part of a more broadly circumscribed Ericaceae as subfam. Monotropoideae (see above).

**Monotropa uniflora** Linnaeus, Sp. pl. 1: 387. 1753. *Hypopitys uniflora* (L.) Crantz, Inst. Rei Herb. 2: 476. 1766. *M. coccinea* Zucc., Flora 15(2): 100. 1832. *M. uniflora* Linnaeus var. *coccinea* (Zucc.) Domin, Sitzungsber. Königl. Böhm. Ges. Wiss. Prag 1915: 5. 1915. Illustrations: R. L. Wilbur & J. L. Luteyn, Ann. Missouri Bot. Gard. 65: 103, fig. 12. 1978. G. D. Wallace, Fl. Neotrop. Monogr. 66: 24, fig. 5. 1995. Figures 1A and 15.

Terrestrial **herbs** 5–30 cm tall, arising from a golden-colored, succulent, highly branched (coralline), brittle, root mass. **Bracts** sessile, elliptic, oblong to lanceolate, 6–16 (20) mm long, (2) 3–5 (10) mm wide, base round-

ed, apex acute, margin entire or somewhat erose. **Inflorescences** somewhat fleshy scapes, (5) 13–30 cm long, glabrous. **Flowers** solitary, nodding at anthesis, the perianth more or less 5-merous, cylindric; sepals 4–5, lanceolate, 13–16 mm long, apex obtuse or acute, margin erose; **petals** 5–8, oblong, obovate or spatulate, 8–16 (20) mm long, apex rounded, margin becoming erose apically, sometimes pubescent within; **stamens** (8) 10 (14), alternately unequal, 7–15 mm long; filaments terete, subulate, pubescent, 11–12 mm long, the bases clasped by elongate, slender, paired, nectariferous lobes; anthers ca. 2 mm diam., reniform, appearing peltate, oriented  $\pm$  horizontally at anthesis; ovary 5–6-locular, globose or ovoid; style 2–7 mm long; stigma 2–6 mm diam., funnel-shaped, obscurely 5-lobed. **Capsule** globose, 7–11 mm long, held erect at maturity, the segments persistent; seeds spindle-shaped, ca. 1 mm long.

*Monotropa uniflora* is distributed in boreal and temperate forests of North America, eastern Asia, Japan, Korea, China, and westward in the Himalayas. In the Neotropics, it is found from Mexico to Colombia, where it forms a mycorrhizal association with a fungus in turn associated with the roots of *Pinus* and/or *Quercus*. In Costa Rica it is found in the shade of humid *Quercus*-forest floors in primary cloud forest and bamboo forest, at 1500–2900 m elevation. It has been found in the Cordillera Tilarán and Cordillera de Talamanca. Flowering specimens have been collected in August through January and March; fruiting specimens in August, November, and December. **Rare/Infrequent.**

*Monotropa uniflora* is characterized by having inflorescences of solitary, nodding flowers that become erect in fruit. The red-flowered color form (= *M. coccinea*) is striking in appearance. In Costa Rica and Panama, virtually all plants are reddish in some part, usually the lower mature stems, but red bracts, calyces, and petals are also known; seemingly no populations are totally white or cream colored. *Monotropa uniflora* is related to *M. hypopitys* L., a species also of boreal and temperate forests of Europe, North America, Asia, and the Himalayas, with neotropical populations found as far south as Guatemala. *Monotropa uniflora* differs from *M. hypopitys* by its single-flowered inflorescences (not several), perianth of sepals (not of distinct sepals and petals), horizontal anthers dehiscent by slits at both ends (not erect and dehiscent only by a single terminal slit), stout style (not slender), elongate and slender nectary lobes (not short and stout), and plants black-drying (not brownish) (see Wallace, 1995; Bidartondo & Bruns, 2001).

## Orthaea Klotzsch

REFERENCES—J. L. Luteyn, *Orthaea* (Ericaceae-Vaccinieae): New species and redefinition of the genus. Nord. J. Bot. 7: 31–37. 1987.

Low, frequently epiphytic **shrubs**. **Leaves** alternate, short-petiolate, the blades coriaceous to subcoriaceous, the margin entire, the venation pinnate or plinerved. **Inflorescences** axillary, racemose, subfasciculate or 1–2-flowered; floral bract minute (in ours) to sometimes large and showy, but usually caducous; pedicels articulate with calyx; bracteoles 2, usually basal. **Flowers** 5-merous, without odor; calyx synsepalous, tube terete or 3-winged (in ours) and sometimes basally apophysate, limb erect to suberect, usually 5-lobed (3-lobed in ours); **corolla** sympetalous, aestivation valvate, carnose, tubular to subcylindric; **stamens** (8) 10, alternately unequal, usually about  $\frac{1}{3}$  length of corolla; filaments distinct or slightly coherent at base, alternately unequal; connectives lacking disintegration tissue (present in some South American species), lacking spurs; anthers equal or alternately subequal, lacking awns, thecae smooth, tubules 2, distinct, shorter than thecae, dehiscing by terminal or slightly obliquely introrse pores; pollen grains in tetrahedral tetrads, lacking viscin threads; ovary inferior; style filiform, about as long as corolla. **Fruit** a berry; seeds numerous.

*Orthaea* is a neotropical genus of ca. 34 species distributed from Mexico to Bolivia and east to Guyana and Trinidad. The genus is characterized by stamens that are about  $\frac{1}{3}$  the length of the corolla and among themselves alternately unequal (the filaments alternately unequal), short anther tubules, and an inferior ovary. The genus has not yet been found in Costa Rica. *Orthaea* is morphologically similar to *Cavendishia*, both having alternately unequal stamens and similar habits. *Orthaea* differs from *Cavendishia* most prominently by its usually shorter stamens with regard to the corolla (ca.  $\frac{1}{3}$  the length vs. equaling the corolla length), anthers of basically equal lengths (unequal in *Cavendishia*), and usual absence of showy floral bracts (present in *Cavendishia*). On the basis of gross morphology, Luteyn (1987b) redefined the genus *Orthaea*, recognizing the new subgenus *Lysiclesia*, in which our species belongs.

***Orthaea panamensis*** (Luteyn & Wilbur) Luteyn, Nord. J. Bot. 7: 33. 1987. *Lysiclesia panamensis* Luteyn & Wilbur, Brittonia 29: 261, fig. 2. 1977. Figure 1H.

Lax, somewhat scandent, almost vine-like **shrubs**; mature stems terete to bluntly angled, smooth, short-pilose, glabrescent, glaucous. **Leaves** with petioles subterete, flattened adaxially, rugose, 2.5–3 mm long, ca. 1 mm diam.,

short-pilose; leaf blades ovate-elliptic, (2.5) 3–3.5 cm long, (1.2) 1.5–2 cm wide, base obtuse or rounded, apex abruptly short-acuminate and apiculate, glabrous, obscurely 3 (5)-plinerved, midrib nearly plane above but raised beneath, lateral nerves and reticulate veinlets slightly raised and prominent above, obscure beneath. **Inflorescences** axillary, racemose, 2–3-flowered; rachis bluntly angled, 1.5–2.2 cm long, ca. 1 mm diam., short-pilose and also bearing scattered, capitate-glandular trichomes ca. 1 mm long; floral bract lanceolate, ca. 1.5 mm long, ciliate; pedicels subterete, 15–17 mm long, ca. 1 mm diam., short-pilose and also bearing scattered, capitate-glandular trichomes; bracteoles medial, strongly nerved, ovate-lanceolate, 3–4 mm long, ca. 1.5 mm wide, acuminate, ciliate and also bearing capitate-glandular trichomes. **Flowers** with calyx 36–48 mm long, short-pilose externally and internally, tube ca. 4–6 mm long but obscured by wings, limb short-campanulate, ca. 2 mm long, conspicuously 3-parted, lobes triangular, acuminate, 25–38 mm long, basally ca. 10–14 mm wide, with margins and lamina bearing scattered capitate-glandular trichomes, sinuses acute; **corolla** membranous, bistratose, cylindric, narrowing to throat, ca. 35 mm long, pink, short-pilose externally (except at base) and internally and at throat, lobes flaring, triangular, ca. 1 mm long, obtuse; **stamens** alternately ca. 10 mm and 12 mm long; filaments alternately ca. 5 mm and 8.5 mm long, distinct, pilose apically; anthers very slightly unequal, alternately ca. 5 mm and 5.5 mm long, thecae 2.5–3 mm long, tubules 2.5–3 mm long, with terminal pores or in shorter stamens slightly obliquely introrse pores; style ca. 36 mm long, pilose apically. **Berry** not seen.

*Orthaea panamensis* is found in premontane cloud forests, 900–1200 m elevation. It is endemic to Panama and is known only from a few localities in western and central Panama. It has not yet been collected in Costa Rica. Flowering specimens have been collected in October, December, and February; fruit are unknown. **Rare/Infrequent.**

*Orthaea panamensis* is characterized by its calyx limb, which has three very large, bract-like lobes instead of the usual five smaller lobes. This is a striking feature that defines *Orthaea* subgen. *Lysiclesia* (A. C. Smith) Luteyn (Luteyn, 1987b) and immediately allows one to recognize the taxon. Only three species are found in this subgenus, the other two being known only from north-central Colombia (Antioquia Dept.). The three species are closely related and possibly even conspecific; more collections of all three species are needed to determine their circumscription and relationships.

***Pernettya* Gaudich.**  
nom. & orth. conserv.

REFERENCES—H. O. Sleumer, Taxonomy of the genus *Pernettya*. Bot. Jahrb. Syst. 105: 449–480.

1985. D. J. Middleton & C. C. Wilcock, A critical examination of the status of *Pernettya* as a genus distinct from *Gaultheria*. Edinburgh J. Bot. 47: 291–301. 1990. J. L. Luteyn, *Pernettya*. Fl. Neotrop. Monogr. 66: 365–383. 1995.

**Terrestrial shrubs.** Leaves alternate, petiolate, the blade coriaceous, the margin entire or often subserrate-crenulate with teeth then bristle-tipped with eglandular or glandular-tipped hairs, glabrous or rarely setose beneath, the venation pinnate. **Inflorescences** axillary, flowers solitary (ours) or in racemes; floral bract and bracteoles indistinguishable; pedicels articulate with calyx, with 2–many bracts along length nearly to apex. **Flowers** 5-merous, nodding, without odor; calyx persistent, synsepalous but parted nearly to base, lobes imbricate at base, normally membranous and not accrescent in fruit, rarely becoming succulent after anthesis but not surrounding fruit; **corolla** sympetalous, aestivation imbricate, lobes reflexed, less than  $\frac{1}{10}$  as long as corolla tube; **stamens** (8) 10, about  $\frac{1}{2}$  as long as corolla; filaments distinct, slightly to conspicuously dilated above base, papillate; connectives with disintegration tissue present abaxially at base of awns, lacking spurs; anthers apically 4-awned, the awns sometimes vestigial (in species from Brazil), thecae minutely papillate at base, dehiscing at apex by introrse, terminal pores; pollen grains in tetrahedral tetrads, lacking viscin threads; ovary superior, 5-locular; style filiform, as long as corolla. **Fruit** a berry, subglobose to globose, apically depressed, glabrous to densely short-pubescent; seeds wingless, numerous, small.

*Pernettya* consists of about 14 species distributed in Tasmania, New Zealand, and Mexico to Argentina. One species occurs in Costa Rica. *Pernettya* is characterized by a superior ovary and baccate fruit. It is closely related to *Gaultheria*, the primary distinction being the baccate fruit of *Pernettya* vs. the capsular fruit of *Gaultheria* (see discussion above under *Gaultheria*).

***Pernettya prostrata*** (Cav.) DC., Prodr. 7: 609. 1839. *Andromeda prostrata* Cav., Icon. 6: 43, t. 562, f. 2. 1801. *P. coriacea* Klotzsch, Linnaea 24: 85. 1851. *P. setigera* Klotzsch, Linnaea 24: 85. 1851. *P. congesta* Klotzsch in Ørsted, Amér. Centr. 9: 1863, nom. nud. *P. oerstedia* Klotzsch in Ørsted, Amér. Centr. 9: 1863, nom. nud. *P. ciliaris* D. Don ex G. Don var. *alpina* J. D. Smith, Bot. Gaz. 25: 148. 1898. *G. alpina* (J. D. Smith) Sleumer, Notizbl. Bot. Gart. Berlin-Dahlem 13: 207. 1936. Illustrations: R. L. Wilbur & J. L. Luteyn, Ann. Missouri Bot. Gard. 65: 106, fig. 13. 1978 (as *P. coriacea*). J. L. Luteyn, Fl. Neotrop. Monogr. 66: 367, fig. 1C, M, and 374, fig. 3A–E. 1995. Figures 1F and 4.

Prostrate and stoloniferous, to erect or ascending shrubs, sometimes forming dense tufts or extensive mats (0.1) 0.2–1 (3) m tall; mature stems terete to subterete, sometimes sharply angled, glabrous or weakly to densely puberulous or laxly crisped pilose, and also usually moderately to densely strigose or hirsute-setose with basally swollen ferruginous, appressed or spreading eglandular and/or rarely gland-tipped hairs 0.5–3 mm long. **Leaves** with petioles 1–4 mm long, often canaliculate adaxially, glabrous to puberulous above; leaf blades subcoriaceous to coriaceous, narrowly to broadly elliptic, oblong, or ovate-oblong to linear-oblong, (2) 6–14 (40) mm long, (2) 4–7 (12) mm wide, base rounded, obtuse, attenuate or cuneate, apex obtuse, acute or subacuminate, midrib rarely protracted into an achlorophyllous mucro, rarely short-mucronate or rounded, margin slightly to conspicuously thickened, usually slightly revolute, minutely crenate-serrulate with 6–12 (17) caducate teeth per side, these bristle-tipped or gland-tipped and 0.2–0.3 mm long, to hirsute-setose and eglandular to 2 mm long, blades themselves usually glabrous or rarely weakly short-pilose along the basal half of midrib above, rarely strigose beneath. **Inflorescences** with 5–10 ovate, ciliate, appressed, persistent bractlets at base of pedicel and 1–6 undifferentiated bractlets scattered along pedicel, these bractlets (1.5) 2–4 mm long; pedicels (1) 4–10 (13) mm long, glabrous or puberulous, sometimes also bearing short-strigose or hirsute-setose, straight or crisped, eglandular or gland-tipped hairs. **Flowers** with calyx lobes ovate to ovate-lanceolate, 2–4 mm long, apex acuminate to acute, weakly to densely ciliate, sometimes also basally with short, gland-tipped hairs; **corolla** cylindric to campanulate-urceolate, (3.5) 5–6 (7) mm long, 2.5–5 mm diam. at base, white to rose tinted, lobes 1–1.5 mm long; **stamens** with filaments 1.5–3 mm long, glabrous or rarely pilose; ovary glabrous to densely short-pubescent; style 2–4 mm long, glabrous or rarely short-pilose in lower half. **Berry** subglobose, 6–16 mm diam., glabrous to densely short-pubescent, dark blue-black, rarely light purple to almost white.

*Pernettya prostrata* is found in montane cloud forest, scrub vegetation, subpáramo to páramo, frequently as a pioneer species in new habitats, (900) 2000–3800 m elevation. It is distributed from Mexico to northwestern Argentina. In Costa Rica it is common at higher elevations of the Central Valley volcanoes and the Cordillera de Talamanca. Flowering and fruiting occur throughout the year. **Common.**

*Pernettya prostrata* is characterized by its usually strigose to setose mature stems, the trichomes having swollen bases, an obtuse to acute (rarely mucronate-tipped) leaf apex, eglandular pubescence, glabrous filaments, and essentially Andean distribution. It is morphologically highly variable with regard to habit, leaf size and shape, stem and leaf indumentum, calyx lobe succulence, and fruit color. Also, because of its broad geographical distribution and often isolated populations, many dif-



ferent names have been assigned to the different populations; Costa Rican populations have traditionally been named *P. coriacea*. After studying the species from throughout its entire geographical range with abundant herbarium material, Luteyn (1995) was not able to see any morphological variation that consistently correlated with geography, geology, elevation, habitat, habit, etc. Since virtually any character might appear anywhere in the range of the species, *P. prostrata* was best treated as a polymorphic species of wide distribution. In Costa Rica, in the páramo vegetation on Cerro de La Muerte and Cerro Chirripó at 3300–3800 m, one puzzling variant may be seen in high-elevation populations, where plants may have distinctly and persistently mucronate leaf apices, a feature otherwise found only in *P. howellii* Sleumer (Galápagos Isl.) and some of the temperate Chilean/Argentinean species. However, although distinctive, this character is not even consistent within a population, and some young leaves with mucronate leaf tips may lose this feature with age.

*Pernettya prostrata* is most closely related to *P. hirta* (Willdenow) Sleumer, which is known only from one small area east of Bogotá, Colombia.

*Pernettya prostrata* is often confused with *Vaccinium floribundum*, both in the field and in herbarium material. However, closer examination of even sterile material shows easily discernible differences: *Pernettya prostrata* has usually strigose-setose mature stems with thick trichomes that have swollen bases; the leaf margins are slightly revolute beneath and of the same color as the lamina proper; the midrib and lamina are the same color on the lower surface of the leaf; and the ovary is superior with the berry subtended by the calyx lobes, whereas *Vaccinium floribundum* has glabrous or short-pilose mature stems; the leaf margins are flat, thickened, smooth in texture, and of a conspicuously lighter color than the leaf lamina proper; the midrib is also a lighter color than the lamina; and the ovary is inferior with the berry having calyx lobes at the apex. Flowers of *P. prostrata* are visited by the bee *Bombus ephippiatus* in Costa Rica (Luteyn, 1998). The berries are reportedly toxic in quantity (but see Luteyn, 1995).

## Psammisia Klotzsch

REFERENCES—A. C. Smith, The American species of Thibaudieae. Contrib. U.S. Natl. Herb. 28: 311–547. 1932 (*Psammisia*, pp. 384–406). J. L. Luteyn, New species and notes on Neotropical Ericaceae. Opera Bot. 92: 109–130. 1987a (*Psammisia*, pp. 120–121). J. L. Luteyn, Ericaceae. Fl. Ecuador 54: 1–406. 1996 (*Psammisia*, pp. 164–209).

Epiphytic shrubs. Leaves alternate (in ours) to subopposite, petiolate, the blades coriaceous, the margin entire, the venation plinerved or pinnate. Inflorescences axillary (in ours) or terminal, subfasciculate or racemose, few- to many-flowered; floral bract small, inconspicuous; pedicels articulate with calyx; bracteoles 2, usually basal. Flowers 5-merous, without odor; calyx synsepalous, tube terete and rarely winged, limb erect or spreading; corolla sympetalous, aestivation valvate, carinate, subcylindric, elongate-urceolate or subglobose; stamens 10, equal,  $\frac{1}{3}$  to nearly as long as corolla; filaments distinct or connate; connectives lacking disintegration tissue, but all laterally or apically 2-spurred, or alternately spurred, or rarely spurs obscure or lacking, when present the spurs either acute and conspicuous or rounded and not very apparent; anthers rigid, lacking awns, thecae conspicuously papillate, tubules 2, distinct, rigid,  $\frac{1}{4}$  to about as long as thecae, dehiscent by elongate, introrse clefts; pollen grains in tetrahedral tetrads, lacking viscin threads; ovary inferior; style filiform, exserted, glabrous. Fruit a leathery berry, green to green speckled with brown.

*Psammisia* consists of approximately 70 species distributed from Mexico to Bolivia and east to Guyana, Amazonian Brazil, and Trinidad. The genus is characterized by having stamens of equal lengths but only  $\frac{1}{3}$  to nearly as long as the overall corolla length; their connectives are usually spurred; the anther tubules are often short, elongate-conical, rigid, and distinct; and an inferior ovary is present. There are three species in Costa Rica. *Psammisia* is related to *Macleania*, differing most conspicuously by its spurred stamens (spurs absent in *Macleania*) and anther tubules that are distinct to the base (not connate). The genus is currently being revised by J.L.L.

Key to the Species of *Psammisia*

- 1a. Rachis elongate, at anthesis 2–6 cm long, the inflorescence distinctly racemose; bracteoles 3 mm long ..... *P. williamsii*
- 1b. Rachis short, at anthesis ca. 0.7–2 cm long or less (elongating in fruit up to 4 cm long), the inflorescence short-racemose but often appearing fasciculate or corymbose by elongation of lower pedicels; bracteoles 2.5 mm long or less ..... 2
- 2a. Staminal filaments typically connate over entire length; anther connectives spurred; inflorescence parts lacking exudate; pedicels 8–25 mm long ..... *P. ramiflora*
- 2b. Staminal filaments distinct or only slightly connate at base; anther connectives lacking spurs; inflorescence parts (especially calyx) with white, scale-like or crystalline exudate (most conspicuous when inflorescence young, but usually persistent); pedicels 20–60 (71) mm long ..... *P. ulbrichiana*

***Psammisia ramiflora*** Klotzsch, Linnaea 24: 44. 1851. *Psammisia symphySTEMONA* J. D. Smith, Bot. Gaz. 20: 291. 1895. Figures 2N and 13.

Terrestrial or usually epiphytic **shrubs**; mature stems slender, terete, glabrous. **Leaves** with petioles (3) 5–12 (17) mm long, sometimes narrowly winged apically, glabrous; leaf blades coriaceous to thick-coriaceous but usually drying membranous, oblong or ovate-oblong, 8–19 (27) cm long, 3–7 (11) cm wide, base cuneate to rounded, apex caudate-acuminate, glabrous, 5-plinerved, lateral nerves arising slightly above base and ascending near margins, midrib impressed or flat above and prominently raised beneath, reticulate veinlets conspicuous and raised on both surfaces. **Inflorescences** axillary, subfasciculate or short-racemose, 4–15-flowered, exudates none; rachis usually <1 cm long but elongating to 1–4 cm long after anthesis, glabrate; floral bract oblong or triangular, (1) 3–4 mm long, often persistent; pedicels 8–25 mm long, often elongating after fruit; bracteoles supramedial, 1.5–2.5 mm long. **Flowers** with calyx 5–8.5 mm long, tube subcylindric or broadly obconic, ca. 2–4 mm long, glabrous, dark green, limb spreading-campanulate at anthesis but becoming erect and cylindric after anthesis forming a persistent crown on maturing ovary, 3–5.5 mm long, light green, lobes triangular to ovate, ca. 1.5–2 mm long, apex acute to rounded and short-apiculate, sinuses rounded to sometimes apparently tearing and then acute; **corolla** parchment thin (thinly fleshy when fresh), unistratose, cylindric throughout, tapering to throat, sometimes slightly constricted below middle, 28–35 mm long, 6–10 mm diam. medially and at base but contracted to 4–5 mm diam. at throat, orange to red with a white tip, throat often with appressed glandular trichomes 0.1–0.4 mm long, lobes oblong, 2.5–3.5 mm long; **stamens** 8–10 mm long; filaments 3.5–4.5 mm long, connate for their entire length, lightly coherent near base only, sometimes completely separate, short-pilose adaxially or along margin in apical free part; connectives apically and alternately unequally 2-spurred, ciliate with trichomes ca. 0.2 mm long; anthers 5.8–7.7 mm long, thecae 3–5.3 mm long, tubules 2–3.5 mm long. **Berry** subglobose, 8–15 mm diam., crowned by persistent calyx limb that may elongate to 7 mm long.

*Psammisia ramiflora* is found in lowland rain forest and premontane and montane cloud forest,

200–2200 m elevation. It is distributed in Guatemala (one collection), Costa Rica, and Panama. Flowering occurs in nearly every month; fruiting specimens in June and December. **Common.**

*Psammisia ramiflora* is characterized by its short-racemose inflorescence that often appears fasciculate or corymbose because of the elongation of the lower pedicels, spurred anther connectives, inflorescence parts without exudate, pedicels 8–25 mm long, and proportionally long corolla lobes. It is variable in leaf size, texture and venation, corolla color, and degree of connation (or lack thereof) of the staminal filaments. Typically, in Costa Rica, the leaf blades are subcoriaceous when fresh, but they dry membranous, the leaf venation is strongly 3 (5)-plinerved with the inner pair of lateral nerves distinct and conspicuous to the apical tip on both surfaces, and the tertiary veinlets are prominent beneath, running perpendicular to the midrib and inner laterals. The leaf veins are also lighter in color than the blade proper when dry. The calyx limb and lobes are usually a distinctly lighter shade of green when fresh as well as a lighter shade of brown when dry. Also, the corolla is red, with a white throat and lobes, and the filaments are usually connate.

*Psammisia ramiflora* is related to *P. ulbrichiana*, a species disjunct from Colombia and Ecuador, and until now has been consistently confused with it. They may be distinguished by the characters mentioned in the key above, with the presence of a white, crystalline exudate being especially noticeable in *P. ulbrichiana*. The species is visited by the hummingbird *Doryfera ludovicae veraguensis* and by the genus *Phaethornis* (pers. observ.; Luteyn, 1998). The flowers are somewhat pungent to the taste (they contain oxalic acid) and are said to give energy when eaten.

***Psammisia ulbrichiana*** Hoerold, Bot. Jahrb. Syst. 42: 306. 1909. Figure 13.

Terrestrial or epiphytic **shrubs**, sometimes with scandent stems. **Leaves** with petioles 8–19 mm long, glabrous; leaf blades ovate, elliptic or oblong-lanceolate, (15) 18–40 cm long, 6–13 (17.5) cm wide, base cuneate to rounded, often  $\pm$  abruptly short-acuminate, apex tapering and long-acuminate, glabrous, 5–7-plinerved. **Inflorescences** axillary, short-racemose but conspicuously corymbiform by elongation of lower pedicels, 10–20 (35)-flowered; rachis 0.7–2 cm long, elongating to 4 cm in fruit, glabrous, although often covered with a scaly or crystalline, white exudate when young which may persist to anthesis; floral bract broadly ovate to oblong, 3–3.6 mm long, apex acute, margin deciduously glandular-fimbriate; pedicels 20–60 mm long, sometimes elongating to 71 mm post-anthesis; bracteoles medial to supramedial, triangular, ca. 1.8–2.5 mm long, apex acute, margin glandular-fimbriate. **Flowers** with calyx 6.5–9 mm long, tube campanulate, the base narrowing and rounded or sometimes truncate, 2.5–4 mm long, limb 4–5.5 mm long, lobes ca. 2–4 mm long, broadly ovate, round, apiculate, margin often appearing irregularly torn, sinuses acute; **corolla** cylindric, swollen in basal  $\frac{1}{3}$ – $\frac{1}{2}$ , conspicuously once-constricted below middle (best seen when fresh), (18) 25–38 mm long, ca. 6 mm diam. near base, glandular-fimbriate apically, dark rose-red in basal swollen part and lighter rose-red apically, lobes 2–3 mm long, triangular to oblong, acute; **stamens** 9–15 mm long; filaments distinct or slightly connate at base, 3–6 mm long, sparsely pilose at margins apically; connectives lacking spurs or with short (minute, vestigial) spurs; anthers 10–13 mm long, thecae 4–7 mm long, tubules sometimes laterally connate in basal half, 3–5.5 mm long. **Berry** slightly depressed-spherical, 13–18 mm diam.

*Psammisia ulbrichiana* is found in premontane cloud forest, 900–1200 m elevation. It is distributed from Costa Rica to Peru. Flowering specimens have been collected in July; fruiting collections in August. **Rare/Infrequent.**

*Psammisia ulbrichiana* is characterized by its large, 5–7-plinerved leaves; short-racemose inflorescence that is conspicuously corymbose because of the elongation of the lower pedicels; the constricted (submedially) corolla; anther connectives lacking spurs; inflorescence parts with white, scale-like or crystalline exudate (most conspicuous when the inflorescence is young, but usually persistent); and pedicels 20–60 (71) mm long. In Costa Rica and Panama, it is morphologically similar to and has been confused with *P. ramiflora*, as described above. The species is visited by hummingbirds in Ecuador (pers. observ.).

**Psammisia williamsii** A. C. Smith, Ceiba 1: 62. 1950. Figure 13.

Epiphytic **shrubs** 1–1.5 m tall; mature stems terete, glabrous. **Leaves** with petioles subterete, rugose, 8–11 mm long and ca. 2 mm diam; leaf blades subcoriaceous, narrowly oblong-elliptic, 10–20 cm long, 3–8.5 cm

wide, base  $\pm$  attenuate and decurrent onto petiole, apex acuminate, 5-plinerved, midrib strongly impressed above and prominent beneath, thickened in basal 1–1.5 cm, lateral nerves and reticulate veinlets inconspicuous. **Inflorescences** axillary, racemose, 5–7-flowered; rachis 2–6 cm long, striate, circumscribed at base by many papery bracts ca. 2 mm long; floral bract oblong-deltate, 4–5 mm long, apex acute; pedicels rugulose, 30–37 mm long; bracteoles basal, ca. 3 mm long. **Flowers** with calyx ca. 9 mm long and 10 mm apical diam., tube cupuliform, inconspicuously glandular, ca. 4 mm long and 5 mm diam., limb spreading-erect, slightly longer than tube, lobes deltate, apiculate, ca. 1 mm long, sinuses concave to complanate; **corolla** carnose, cylindric but slightly swollen below middle, conspicuously and abruptly constricted at throat, ca. 35 mm long, ca. 10–12 mm diam. near base, red with yellowish throat and lobes, the lobes oblong-deltate, obtuse, 2–3 mm long; **stamens** 10–11 mm long; filaments distinct, ca. 5 mm long; connective carnose and apically 2-spurred, the spurs spreading, obtuse; anthers 9–10 mm long, thecae ca. 1.5 mm diam., shortly incurved at base, tubules scarcely 2 mm long, much shorter than thecae, dehiscing through oval rims. **Berry** not seen.

*Psammisia williamsii* is found in premontane cloud forest, 1800–2100 m elevation. It may be endemic to Costa Rica and is known with certainty only from the type collection and Luteyn *et al.* 4526 (both Cartago Province, El Muñeco area). A recent collection from Chiriquí Province, Panama (Fortuna Dam site area), Luteyn & Pedraza 15550, may also be this species; that collection has vegetative and inflorescence features including the color combination of the corolla of *P. williamsii*, but unfortunately it is only in bud. Flowering specimens have been collected (in Costa Rica) only in December; fruits are unknown. **Endangered.**

*Psammisia williamsii* is characterized by its racemose inflorescence with an elongate rachis (at anthesis 2–6 cm long) and large, carnose corollas. It is morphologically similar to *P. ramiflora* and *P. ulbrichiana* but differs by a longer and racemose inflorescence with a longer rachis, longer bracteoles and larger flowers, and its corollas, which have a different shape and color combination. These character differences are slight, however, and more collections of *P. williamsii* are needed before its range of morphology and specific relationships can be determined. The species is visited by hummingbirds (pers. observ.).

## Satyria Klotzsch

REFERENCE—J. L. Luteyn, New species and notes on Neotropical Ericaceae. Opera Bot. 92: 109–130. 1987 (*Satyria*, pp. 121–122).

Epiphytic or terrestrial **shrubs**. **Leaves** alternate, evergreen, petiolate, the blades coriaceous, the margin entire, the venation usually plinerved (in ours), rarely pinnate. **Inflorescences** axillary, racemose or subfasciculate, often ramiflorous and then 1-several arising from a callus-like mound; floral bract small, inconspicuous, usually persistent; pedicels articulate with calyx; bracteoles 2, usually persistent. **Flowers** 5-merous, without odor; calyx synsepalous, tube subglobose to shortly campanulate, limb flaring or spreading, lobes (3–4) 5, ovate to triangular or merely apiculate; **corolla** sympetalous, aestivation valvate, carinose, cylindric to narrowly vasiform, lobes triangular to narrowly oblong, acute; **stamens** 10, of alternately unequal lengths, usually about  $\frac{1}{2}$  as long as corolla; filaments equal and firmly connate into a tube for more than half their length, membranous to thinly coriaceous; connectives lacking disintegration tissue or spurs; anthers basifixed, firm, alternately unequal in length, lacking awns, slightly dimorphic in shape, the longer ones spreading apically with tips often incurved and decorated in a dendritic pattern and with tubules twisted so dehiscence latrorse, the shorter ones laterally coherent apically, tips straight, often not ornate, tubules straight so dehiscence introrse, thecae subcoriaceous, slightly to not papillate, tubules 2, distinct, not sharply differentiated from thecae, dehiscing by subapical pores; pollen grains in tetrahedral tet-

rads, lacking viscin threads; ovary inferior; style filiform, as long as corolla or slightly exserted, glabrous; stigma usually truncate; nectariferous disc usually conspicuous, annular-pulvinate. **Fruit** a spherical berry, dark blue-black (in ours), rarely translucent white; seeds numerous.

*Satyria* consists of about 25 species distributed from southern Mexico to Bolivia and east to French Guiana. Four species are currently known to occur in Costa Rica. *Satyria* is characterized by its numerous, usually ramiflorous inflorescences; alternately unequal stamens (equal filaments, unequal anthers) that are about  $\frac{1}{2}$  as long as the corolla; entirely connate staminal filaments; and inferior ovary. Morphology as well as molecular data (but see Kron et al., 2002b) indicate that the genus is related to *Cavendishia* and *Orthaea*, two other vaccinioid genera with alternately unequal stamens (each with unequal filaments). *Satyria* is currently being revised in a Ph.D. study by E. Ann Powell (Wake Forest University).

**Key to the Species of *Satyria***

- 1a. Inflorescence clearly long-racemose; corolla glabrous or usually puberulent over entire length; corolla red, greenish toward apex, often bluntly 5-angled; lowland, primary rain forest to premontane cloud forest ..... *S. pauurensis*
- 1b. Inflorescence fasciculate to short-racemose; corolla glabrous or rarely shortly and sparsely puberulent apically; corolla red or orange, white or green toward apex, terete to bluntly 5-angled; premontane to montane cloud forest ..... 2
- 2a. Corolla (15) 17–36 mm long; leaves (6) 10–27 (30) cm long; inflorescences 3–11 (30)-flowered, fasciculate to short-racemose ..... 3
- 2b. Corolla 7–21 mm long; leaves 6.5–18 (25) cm long; inflorescences 6–16-flowered, short-racemose ..... 4
- 3a. Corolla cylindrical throughout or only somewhat swollen toward the base, red to rose-red becoming white at throat and lobes; rachis 0.5–1.5 (4) cm long ..... *S. warszewiczii*
- 3b. Corolla conspicuously swollen in basal  $\frac{1}{4}$ – $\frac{1}{2}$ , red becoming green at throat and lobes; rachis 0.5–0.9 cm long ..... *S. ventricosa*
- 4a. Leaves conspicuously bullate, the inner pair of lateral nerves arising from about or just below the middle; calyx lobes conspicuous, ovate to triangular, ca. 2–2.3 mm long; corolla 7–11 mm long, conspicuously swollen and globose basally then abruptly constricted and cylindrical apically .... *S. species "A"*
- 4b. Leaves flat, not bullate, the inner pair of lateral nerves arising near base; calyx lobes inconspicuous, apiculate, ca. 0.2–0.8 mm long; corolla 10–21 mm long, cylindric and of equal diameter along entire length ..... 5
- 5a. Leaf blades 4–9 (11) cm wide; calyx lobes triangular-apiculate, ca. 0.2–0.3 mm long; corolla 10–15 mm long; Guatemala to western Costa Rica ..... *S. meiantha*
- 5b. Leaf blades 2–3 cm wide; calyx lobes ovate-apiculate, 0.5–0.8 mm long; corolla 15–21 mm long; western Panama ..... *S. species "B"*

**Satyria meiantha** J. D. Smith, Bot. Gaz. 47: 256. 1909. Figure 15.

Usually epiphytic **shrubs**. Leaves with petioles stout, 7–20 mm long, 2–3 mm diam., glabrous; leaf blades elliptic, lance-ovate, oblong or ovate-oblong, (8) 12–18 (25) cm long, 4–9 (11) cm wide, base usually cuneate to rounded, apex acuminate to acute, glabrous, 3 (5)-plinerved with inner pair of lateral nerves arising in basal 15 mm, midrib thickened and raised in basal 10–15 mm above, then apically thinner and becoming slightly impressed near apical tip, raised and conspicuous beneath, lateral nerves slightly raised but inconspicuous above becoming slightly impressed like midrib near apical tip, raised and conspicuous beneath, reticulate veinlets slightly raised but inconspicuous on both surfaces. **Inflorescences** short-racemose, 6–12-flowered, frequently up to 7 together, ramiflorous from callus at leafless nodes on older branches (persisting over many years); rachis angled, striate, 5–15 mm long, puberulent, inconspicuously short-glandular-fimbriate; floral bract oblong-ovate, deciduous, <2 mm long, apex acute to acuminate, glabrous or puberulent, margin deciduously glandular-fimbriate; pedicels 6–18 mm long, glabrous or minutely puberulous, glandular-fimbriate especially apically near articulation; bracteoles at basal  $\frac{1}{2}$  to middle of pedicels, oblong-ovate, ca. 1.5 mm long, apex acuminate, glabrous or puberulent, margin deciduously glandular-fimbriate. **Flowers** with calyx 3.5–5.5 mm long, glabrous or minutely puberulous, glabrate, with or without glandular fimbriae 0.1–0.2 mm long, tube cylindric-campanulate, 2–2.5 mm long, ca. 2 mm diam., limb erect to spreading, 1.5–3 mm long, lobes triangular, apiculate, ca. 0.2–0.3 mm long, sinuses flat to rounded; **corolla** coriaceous, thinly bistratose, tubular but slightly swollen at base and contracted apically, broadly and bluntly pentagonal, rarely slightly zygomorphic, ca. 20 mm long and ca. 6 mm diam. when fresh, but drying 10–15 mm long and 2–4 mm diam., basal  $\frac{1}{4}$  rose-red becoming white in apical  $\frac{1}{4}$ , glabrous or densely but minutely puberulous, also typically with inconspicuous reddish, glandular fimbriae ca. 0.1 mm long, lobes oblong, acute, 1–2 mm long; **stamens** alternately 6.6–9 mm and 7.6–10 mm long; filaments ca. 4–5 mm long, equal, connate into a tube, apically, abaxially and marginally short-pilose onto connectives, also bearing glandular fimbriae apically; anthers alternately 4.2–5.5 mm and 5.2–6.5 mm long, thecae alternately ca. 3–3.5 mm long and 3.5–4.5 mm long, tubules apically alternately straight and slightly flaring ca. 1.6–2.5 mm long, dehiscing by clefts ca. 1–2 mm long. **Berry** globose, to at least 8 mm diam., turning purple.

*Satyria meiantha* is found in premontane cloud forest, 850–1700 m elevation. It is distributed in Guatemala, Nicaragua, and Costa Rica, where it is limited to the Cordillera Tilarán. Flowering specimens have been collected in January–April, August, and October; fruiting in June, October, and November. **Locally Common.**

*Satyria meiantha* is characterized by having inflorescences that are axillary or frequently ramiflorous, short-racemose, glabrous rachises, glabrous

or rarely shortly and sparsely puberulent apically corollas that are red becoming white apically, and a premontane to montane cloud forest habitat. It is morphologically similar to *S. warszewiczii*, and the small differences given in the key may not stand rigorous analysis; more fieldwork is needed to compare the two. The species is visited by the hummingbird *Lampornis calolaema* (male) in Costa Rica (pers. observ.; Luteyn, 1998).

**Satyria panurensis** (Benth. ex Meissn.) Benth. & Hook.f. ex Niedenzu, Bot. Jahrb. Syst. 11: 249. 1890. *Thibaudia panurensis* Benth. ex Meissn. in Martius Fl. Brasil. 7: 125. 1863. *S. panurensis* (Benth. ex Meissn.) Benth. & Hook.f., Gen. Pl. 2: 568. 1876, nom. illeg. *Riedelia panurensis* (Benth. ex Meissn.) Kuntze, Rev. Gen. Pl. 2: 384. 1891. *S. elongata* A. C. Smith, Contrib. U.S. Natl. Herb. 28: 521. 1932. *S. triloba* A. C. Smith, Contrib. U.S. Natl. Herb. 28: 523. 1932. Figures 1G and 15.

Epiphytic, lianoid **shrubs**; mature stems terete, striate, glabrous. **Leaves** with petioles 4–6 (9) mm long, subterete, rugose, weakly puberulent; leaf blades ovate to oblong, 10–13 (22.5) cm long, 3–6 (7) cm wide, base rounded, subcuneate, or subcordate, apex acuminate, glabrous, nitid, 3–5-plinerved with nerves arising from near base and spreading near margins, midrib slightly raised above, prominent beneath, lateral nerves slightly raised to plane above and raised beneath, reticulate veinlets slightly raised on both surfaces, conspicuous to obscure. **Inflorescences** axillary, racemose, 8–20-flowered; rachis 1.5–4.5 cm long, subterete, bluntly angled, striate, puberulent; floral bract ovate, 2–3.7 mm long, apex acute-acuminate, glabrous or puberulent at base, margin ciliolate and minutely glandular-fimbriate; pedicels 8–13 mm long, subterete, subrugose, striate, glabrous or puberulent; bracteoles nearly base, ovate, 1–2 mm long, apex acute-acuminate, densely puberulent or glabrous, margin sparsely glandular-fimbriate. **Flowers** with calyx 3–4 mm long, tube subcylindric, sparsely to densely puberulous, 1.5–2 mm long, limb 1–2 mm long, spreading-campanulate, often rotate to reflexed, lobes oblong-ovate, 0.5–1 mm long, apiculate, often irregularly divided or fused, the margins often torn or thinner in texture, sinuses acute; **corolla** thin-carnose, thinly unistratose, tubular but gradually narrowing apically, pentagonal, 16–34 mm long, 3–5 mm diam. near base, glabrous or usually puberulent, dull dark red to scarlet, lobes ca. 1.5–4 mm long, reflexed, oblong, subacute, greenish; **stamens** alternately 7.5–10 mm and 8.5–11 mm long; filaments 4–6 mm long, equal, glabrous, produced into slender connectives, these minutely pilose with hairs up to 0.2 mm long; anthers alternately 4.8–7 mm and 6–8 mm long, thecae ca. 3.5–4.5 mm long, elongated at base, tubules ca. 1.5–2.7 mm long, the tips lacking ornamentation, dehiscing by pores 1.5–2 mm long. **Berry** 10–15 mm diam., spherical, glabrous, dark blue-black.

*Satyria panurensis* grows in primary rain forest to premontane cloud forest, 5–850 (1250) m elevation (to 1400 m in Nicaragua). It is scattered on the Caribbean slopes of Mesoamerica from southern Mexico to western Panama, then it is found along the wet Pacific Coast of Puntarenas Province, Costa Rica, and Chocó Depto., Colombia, and finally crosses the Andes occurring mostly in Amazonian rain forest in an arc from Amapá, Brazil, west through the Guianas and south to Peru; it has also been collected in white-sand savannas in Amazonia. In Costa Rica it is infrequently collected on the Caribbean slopes including inundated forest in Limón Province, but then it has also been collected a few times on the wet Pacific slopes of the Osa Peninsula. Flowering specimens have been collected in March, June, July, September, and October; fruiting specimens in January, March, August, October, and November. **Rare/Infrequent.**

*Satyria panurensis* is characterized by having axillary and clearly long-racemose inflorescences, puberulent rachis and (usually) corolla, often bluntly pentagonal corolla that is red basally but becoming greenish apically when fresh, and its lowland, primary rain forest distribution. Morphologically it is without close relatives, perhaps because of its usual isolation in primary lowland rain forest. The taxa called *S. elongata* and *S. triloba* (see A. C. Smith, 1932) are no more than inconsequential variants within this geographical wide-ranging species.

***Satyria ventricosa*** Luteyn, Brittonia 53: 440, fig. 1. 2001.

Lianoid **shrubs** climbing to at least 9 m; mature stems terete to subterete, glabrous; twigs subterete, bluntly angled, somewhat striate, glabrous. **Leaves** with petioles subterete, strongly rugose, (6) 9–15 mm long, slightly winged apically due to decurrent leaf blade, glabrous; leaf blades coriaceous, elliptic to lance-elliptic, (15) 19–27 cm long, (4) 7–14 cm wide, base cuneate, attenuate and shortly decurrent onto petiole to rounded, apex narrowing and very short-acuminate, glabrous on both surfaces but with scattered, minute (ca. 0.1 mm long), reddish, glandular fimbriae beneath, 3 (5)-plinerved with inner pair of lateral nerves arising from (1.5) 2–3 cm above base, midrib conspicuously thickened and raised in basal 2–2.5 cm becoming progressively thinner and plane apically above and conspicuously raised beneath, lateral nerves slightly raised basally becoming weakly impressed apically above and raised beneath, reticulate veinlets plane to weakly impressed above and slightly raised beneath. **Inflorescences** short-racemose, 4–11-flowered, frequently several together, ramiflorous from a callus or at least arising from leafless nodes on older branches (persisting over many years); rachis subterete,

sharply to bluntly angled, 0.5–0.9 cm long, moderately densely glandular-fimbriate otherwise glabrous; floral bract continuous with rachis, persistent, strongly spreading to reflexed, ovate to elliptic-ovate, 1.3–2.5 mm long, margin glandular-fimbriate otherwise glabrous; pedicels thin, striate, 19–21 mm long, glabrous; bracteoles nearly basal, ovate-lanceolate, ca. 0.8–2 mm long, apex short-acuminate, margin glandular-fimbriate otherwise glabrous. **Flowers** with calyx ca. 2–4.5 mm long, sometimes seemingly slightly stipitate, glabrous, tube cylindrical to bluntly pentagonal, rugose, ca. 1–2.5 mm long, basally apophysate, limb rotate-campanulate, often spreading and reflexed, ca. 1–2 mm long, lobes apiculate, to ca. 0.5 mm long, sinuses concave; **corolla** carnose, bistratose, essentially tubular but bluntly pentagonal, conspicuously swollen in basal  $\frac{1}{4}$ – $\frac{1}{3}$  (especially noticeable when fresh), 21–36 mm long, 5–15 mm diam. at base becoming ca. 2–4 mm diam. at throat, glabrous or sparsely short-puberulent in apical half, also bearing few, scattered, glandular fimbriae apically, red at base but becoming green at throat and lobes, lobes erect, ovate, 1.5–3 mm long, apex acute; **stamens** alternately ca. 8–9 mm and 9–10 mm long; filaments equal, connate into a tube ca. 3–4.5 mm long, glabrous below but ciliate apically, also abaxial surface of tube glandular-fimbriate; anthers alternately ca. 4.8–6 mm and 5.5–7 mm long, thecae and tubules nearly indistinguishable and about equal in length, tubules apically acuminate, alternately somewhat ornate. **Berry** not seen.

*Satyria ventricosa* is currently endemic to the Continental Divide, premontane cloud forests of central (Veraguas Prov.) and western (Bocas del Toro and Chiriquí Prov.), Panama, 980–1400 m elevation, where it is known from only about six collections. It has not yet been collected in Costa Rica. Flowering specimens have been collected in February and October; fruits are unknown. **Endangered.**

*Satyria ventricosa* is characterized by having a cauliflorous, subfasciculate to short-racemose inflorescence and by the size, shape, and color patterns of its corolla. It differs from all other species of *Satyria* in Mesoamerica by its large and ventricose-based corolla (up to 13–15 mm basal diam. when fresh). Both *S. ventricosa* and *S. panurensis* have corollas that are red at the base and green apically in the throat and lobes, although they differ in several other features mentioned in the key.

***Satyria warszewiczii*** Klotzsch, Linnæa 24: 22. 1851. *S. clonantha* Klotzsch, Linnæa 24: 22. 1851. *Riedelia warszewiczii* (Klotzsch) Kuntze, Rev. Gen. Pl. 2: 384. 1891. *R. clonantha* (Klotzsch) Kuntze, Rev. Gen. Pl. 2: 384. 1891. *S. ovata* A. C. Smith, Contrib. U.S. Natl. Herb. 28: 524. 1932. Illustration: R. L. Wilbur & J. L. Luteyn, Ann. Missouri Bot. Gard. 65: 118, fig. 15. 1978. Figure 13.

Epiphytic or terrestrial **shrubs**, sometimes lianoid 1–2.5 (4) m long; mature stems stout, terete, glabrous, grayish to brown or reddish-brown. **Leaves** with petioles stout, rugose, (5) 8–22 mm long; leaf blades chartaceous to coriaceous, oblong, ovate-oblong, lance-oblong or elliptic, (6) 10–25 (29) cm long, (2) 4–10 (14) cm wide, base cuneate, rarely rounded, apex acute to acuminate, glabrous or rarely inconspicuously glandular-fimbriate beneath with trichomes 0.2 mm long or less and drying reddish-brown, 3–(5)-plinerved, midrib and lateral nerves slightly raised in basal  $\frac{1}{2}$ – $\frac{1}{3}$  and then apically slightly impressed above, prominently raised beneath, reticulate veinlets slightly raised on both surfaces but usually obscure. **Inflorescences** short-racemose, 3–10 (30)-flowered, frequently several together, ramiflorous from a callus or at least arising from leafless nodes on older branches (persisting over many years); rachis striate, 5–15 (40) mm long, glabrous; floral bract ovate to triangular, (1.8) 2–3 (4.5) mm long, to 4 mm wide, apiculate, inconspicuously ciliate; pedicels terete, often apically swollen, 8–20 (25) mm long, glabrous or rarely sparsely puberulent; bracteoles alternate, narrowly triangular, 1–1.5 (2) mm long, apex acute, inconspicuously ciliate. **Flowers** with calyx 6–7.5 mm long, glabrous or deciduously puberulous, tube cylindric to campanulate, 1.5–3 mm long, occasionally slightly enlarged at base, limb thinly coriaceous, 1.5–4.5 mm long (usually longer and more conspicuous than tube), either spreading-campanulate and apically truncate with lobes not obvious to apiculate and at most 1 mm long, or limb spreading apically with lobes oblong-ovate, conspicuous and strongly reflexed, to ca. 2 mm long, sinuses concave; **corolla** thick-carnose when fresh but often drying thin-membranous, bistratose, cylindric or tapering to slightly flaring throat, occasionally with a somewhat swollen base and apically flaring, (15) 17–35 mm long, mostly (2) 3–4 (6) mm diam., usually bright red in basal  $\frac{1}{4}$  with apex white, rarely shortly and sparsely puberulent apically, lobes oblong, 1–2 mm long, apex acute, white; **stamens** alternately unequal, 6.5–9.5 mm and 7.5–11 mm long; filaments (1.5) 3–5 mm long, the apical free portion weakly ciliate and rarely abaxially bearing a few glandular fimbriae; anthers alternately ca. 3.5–6.5 mm and 4.5–8 mm long, thecae alternately ca. 3.8–5 mm and 4.8–6 mm long, tubules 2.7–4 mm long with oval dehiscence clefts 1.8–2.5 mm long. **Berry** 7–8 mm diam., spherical, blue-black but often glaucous.

*Satyria warszewiczii* is found in premontane and montane cloud forest, (100) 300–2500 m elevation. It is distributed from southern Mexico to Panama. Flowering occurs in all months; fruiting collections March–June and October. **Common.**

*Satyria warszewiczii* is characterized by having axillary or frequently ramiflorous inflorescences that are short-racemose or arise from a low, pad-like mound; glabrous rachis; glabrous or rarely shortly and sparsely puberulent apically corolla, which is red becoming white apically; and its premontane to montane cloud forest habitat. There is considerable morphological variability in the shape and venation of the leaves and in the size

of the flowers in this wide-ranging species. The extremes are striking, but only one species can be recognized, *S. clonantha* and *S. ovata* representing but minor variations. Common names in Costa Rica include *colmillo* and *uva*. The species is visited by the hummingbird *Lampornis calolaema* in Costa Rica (pers. observ.; Luteyn, 1998).

### Satyria species “A”

Terrestrial or sometimes epiphytic **shrubs** to 2 m tall; mature stems terete to subterete, striate, epidermis cracking longitudinally, glabrous, reddish-brown; twigs subterete to complanate, conspicuously bluntly angled, often striate, glabrous, reddish-brown. **Leaves** with petioles subterete, rugose, 5–10 (25) mm long, 1.5–2.5 mm diam., glabrous; leaf blades coriaceous, longitudinally conspicuously bullate, lanceolate to sometimes elliptic-lanceolate, (4) 6.5–10 (13) cm long, (1.5) 2–3.5 (5) cm wide, base cuneate, apex acuminate to short-acuminate, glabrous, deciduously and shortly glandular-fimbriate beneath with usually only blackened bases of trichomes present on mature leaves, 5 (7)-plinerved with inner pair of lateral nerves arising at or a little below the middle, midrib thickened and raised in proximal 3–4 cm especially basal 1.5 cm then plane to slightly impressed apically above and raised beneath, lateral nerves strongly impressed above for entire length and conspicuously raised beneath, reticulate veinlets slightly impressed above but obscure beneath. **Inflorescences** usually arising from axils of leafy nodes (rarely, when epiphytic and in forest canopy, arising from leafless nodes), short-racemose, (3) 6–10 (14)-flowered, circumscribed at base by a series of few, broadly ovate, acute, marginally glandular-fimbriate bracts to ca. 2 mm long and 1–1.5 mm wide; rachis subterete, sharply angled, very congested, ca. 3–6 mm long, glabrous; floral bract narrowly ovate-lanceolate, 2.3–4 mm long, ca. 1 mm wide, apex acuminate, glabrous to ciliate, margin glandular-fimbriate with reddish-brown trichomes <0.5 mm long; pedicels thin, angulate, abruptly swollen at tip and there often hypocrateriform, 15–17 mm long, glabrous or scattered white-puberulent to short-pilose especially at apex, also bearing few, reddish-brown, glandular fimbriae at articulation; bracteoles located medially or submedially, opposite to subopposite, ovate, 0.8–2 mm long, apex acuminate, glabrous to ciliate, margin glandular-fimbriate. **Flowers** with calyx 4–5 mm long, glabrous or white-puberulent, usually separated from pedicel by a 0.5 mm long, constricted stipe after anthesis, tube subcylindric-campanulate, rugose to muricate, ca. 1.7–2.5 mm long, limb spreading-erect, ca. 2.2–3 mm long, lobes triangular to ovate, ca. 2–2.3 mm long, sinuses acute, apparently sometimes tearing slightly at base; **corolla** carnose, bistratose, terete, ca. 7–12.5 mm long overall, conspicuously swollen and globose in basal  $\frac{1}{2}$  where reddish-orange and 4–8.3 mm diam., abruptly cylindrical in apical  $\frac{1}{2}$  where white and ca. 2–4 mm diam., glabrous or white-puberulent externally, glabrous or sparsely white-pilose on lobes internally with translucent hairs to 0.4 mm long, also bearing scattered, reddish-brown, glandular fimbriae apically ca. 0.1 mm long, lobes triangular-ovate, 0.5–1 mm long, apex acute; **stamens** 10, alter-



TABLE 3. Salient morphological differences between *Satyria* species "A" and *S. allenii*.

	<i>Satyria</i> species "A"	<i>Satyria allenii</i>
Petiole length (mm)	5–10 (25)	6–12
Petiole diameter (mm)	1.5–2.5	3–4.5
Petiole indumentum	Glabrous	Pubescent
Leaf blade base	Cuneate	Rounded
Leaf blade margin	Flat	Revolvate
Leaf venation	Inner pair lateral nerves arising from middle; midrib thick and raised in basal 3–4 cm	Inner pair lateral nerves arising from near base; midrib thick and raised at most in basal 5 mm
Inflorescence bracts	2 × 1–1.5 mm	5 × 4 mm
Inflorescence indumentum	Glabrous	Densely short-pilose
Rachis length (mm)	3–6	12–30
Calyx limb shape	Spreading-erect	Rotate-reflexed
Corolla length (mm)	7–12.5	15–17
Corolla shape	Basally globose, apically cylindric	Cylindric throughout

nately ca. 4.6–5.5 mm and 5.3–6 mm long; filaments ca. 2.6–3.2 mm long, glabrous; connectives sparsely ciliate with translucent hairs ca. 0.3 mm long; anthers alternately ca. 2.5–3.2 mm and 3.2–3.8 mm long, thecae alternately ca. 1.5–2 mm and 2–2.5 mm long, tubules ca. 1–1.5 mm long, broadening apically and rounded at apex, basically without ornamentation, the dehiscence clefts about as long as tubules overall. **Berry** not seen.

*Satyria* species "A" is found in lowland rain forest and premontane cloud forest areas in Costa Rica and Panama, (0) 800–1200 (1400) m elevation. In Costa Rica it has been collected only once (Cartago: Turrialba, Parque Nacional Barbilla, Sendero Científico Barthón, *E. Mora* 1972), where it was apparently collected in lowland rain forest at 0 m elevation (fide label). In Panama (Chiriquí: Fortuna Dam site; Veraguas: Cerro Tute; Coclé: El Copé; Panamá: Cerro Campana and Cerro Jefe), it is locally common when found growing terrestrially along open, disturbed roadsides but is rather rare when growing as an epiphyte in closed canopy. Flowering specimens have been collected in January, February, March, September, and October; fruits are unknown. **Locally Common** (in Panama).

*Satyria* species "A" is characterized by its small, proportionally long-petiolate; strongly bulate, lanceolate to elliptic-lanceolate leaves; short-racemose inflorescences found at leafy or leafless nodes; and short corollas that are conspicuously swollen and globose basally and cylindric apically. The swollen nature of the corolla is not easily seen in dried herbarium specimens. The leaves of *Satyria* species "A" often dry a dark reddish-brown color. There seems to be a positive correlation between plants growing in forest with a dense canopy, the epiphytic habit, and inflores-

cences arising from leafless nodes. Plants growing in an open habit are terrestrial and have inflorescences arising from leafy nodes. However, few collections and localities are known for this species. Floral pubescence (i.e., glabrous vs. short-pilose pedicels, calyces, and corollas) seems to vary even within one population growing epiphytically on a single tree (at Cerro Jefe). *Satyria* species "A" is morphologically most similar to and has until now been confused with *S. allenii* A. C. Smith, a species of central Panama (Coclé and Panamá Prov.). Although superficially similar in overall appearance, these two species differ in many features (see Table 3). Its overall relationships, however, await further study. The species is visited by the hummingbird *Lampornis calolaema castaneiventis* in Panama (pers. observ.).

#### *Satyria* species "B"

Terrestrial **shrubs** to 2 m tall; mature stems terete, epidermis cracking longitudinally, glabrous; twigs subterete, bluntly angled, glabrous. **Leaves** with petioles terete, rugose, 6–9 mm long, 1.5–3 mm diam., glabrous; leaf blades coriaceous, lanceolate to elliptic-lanceolate, 6.5–8 cm long, 2–3 cm wide, base cuneate, apex bluntly short-acuminate, glabrous, weakly and thinly glandular-fimbriate on lower surface, 3 (5)-plinerved with all venation relatively inconspicuous and inner pair of lateral nerves arising up to 2 cm above base, midrib thickened and raised above in basal 1.5–2 cm then weakly raised or impressed apically, raised and conspicuous beneath, lateral nerves weakly impressed above and weakly raised beneath,  $\pm$  inconspicuous on both surfaces, reticulate veinlets obscure above and weakly raised to obscure beneath. **Inflorescences** racemose, 7–16-flowered, apparently typically solitary in leafy or leafless nodes but new inflorescences arising from same nodes in successive seasons; rachises subterete, strongly angled, 0.7–2 cm long, glabrous; floral bract ovate-lanceolate, 2–2.5

mm long, ca. 1–1.5 mm broad, apex acuminate, margin glandular-fimbriate, glabrous; pedicels subterete, striate, 10–13 mm long, 1–1.5 mm diam., glabrous; bracteoles subopposite, medial, ovate to lanceolate, 1.2–1.5 mm long, apex acuminate, margin glandular-fimbriate, glabrous. **Flowers** with calyx ca. 3–5 mm long, glabrous, tube cylindric, ca. 1.5–2.6 mm long, ca. 2.5–4.2 mm diam., limb campanulate, ca. 1.5–2.4 mm long, lobes broadly ovate, apiculate, ca. 0.5–0.8 mm long, ca. 2.5 mm wide at base, sinuses concave or sometimes tearing and then acute; **corolla** thin-carnose, bistratose, cylindric throughout but slightly bluntly pentagonal, ca. 15–21 mm long, 4–8.5 mm diam. at base, glabrous, rose-red in basal half and white in apical half, lobes oblong-deltate, ca. 1.5–2 mm long, apex acute; **stamens** 10, alternately ca. 6–6.8 mm and 7–7.8 mm long; filaments ca. 3–3.8 mm long, glabrous or ciliate along apical free portion; connectives marginally short-puberulent; anthers alternately ca. 4–5 mm and 4.8–6 mm long, thecae alternately ca. 2.4–2.8 mm and 3.3–3.5 mm long, tubules alternately ca. 1.5–2.3 mm and 1.6–2.5 mm long, the apical margins bluntly erose. **Berry** immature,  $\pm$  spherical, at least 6 mm diam., green.

*Satyria* species “B” is known only from open, windswept slopes along the edge of premontane cloud forest, at the Fortuna Dam region (Chiriquí Prov.), Panama, 1000–1200 m elevation. It has not yet been collected in Costa Rica. Flowering collections have been made in January and February; immature fruits in mid-January. **Endangered.**

*Satyria* species “B” is characterized by its overall glabrousness; small lanceolate leaves with relatively inconspicuous nervation in general, only the midrib being obvious; short-racemose inflorescences; and corollas that are cylindric throughout their entire length. Morphologically, it is most similar to *S. allenii*, found in central Panama, that species being short-pilose overall and with much larger and broader elliptic leaves with prominent venation.

## Sphyrospermum Poepp. & Endl.

REFERENCE—A. C. Smith, The genera *Sphyrospermum* and *Disterigma*. Brittonia 1: 203–232. 1933.

### Key to the Species of *Sphyrospermum*

- 1a. Leaf blades linear ..... *S. linearifolium*
- 1b. Leaf blades variously shaped but never linear ..... 2
- 2a. Pedicels 1–4 (8) mm long; corolla dark red or maroon, 7–10 mm long, campanulate; berry depressed-globose, quadrangular, translucent pearl-white ..... *S. dissimile*
- 2b. Pedicels 5–25 mm long; corolla white to pinkish (rarely bright red), 2–9 mm long, cylindric to cylindric-urceolate; berry spherical, terete, pale to dark lilac to translucent white ..... 3
- 3a. Corolla 2–3.5 mm long ..... 4

Slender, often straggly, epiphytic or terrestrial **shrubs** with pendent branches. **Leaves** alternate, sessile to petiolate, the blades coriaceous, sometimes very thickly so, often brittle, the margin entire, the venation obscure. **Inflorescences** axillary, flowers solitary or rarely paired; floral bract minute, persistent; pedicels continuous with calyx, slender, pendent, apically swollen; bracteoles 2, basal, deciduous. **Flowers** 4–5-merous, without odor; calyx synsepalous, tube subglobose or obconic, limb suberect; **corolla** sympetalous, aestivation apparently valvate, campanulate, cylindric (tubular), to infundibuliform; **stamens** usually as many or twice as many as corolla lobes, equal or alternately slightly unequal; filaments distinct, usually longer than anther, usually somewhat sigmoid at base; connectives lacking disintegration tissue or spurs; anthers inserted abaxially near base, membranous, lacking awns, thecae minutely papillate, tubules 2, distinct, as long and wide as or longer than thecae, dehiscing by introrse, oval clefts; pollen grains in tetrahedral tetrads, lacking viscin threads; nectariferous disc annular-pulvinate, but not apparent; ovary inferior, the ovules numerous, the placentation axile but often appearing central or even basal, the partitions soon decaying; style filiform, about as long as corolla, rarely slightly exerted, glabrous; stigma truncate. **Fruit** a juicy berry, subglobose or ellipsoid, translucent white to lavender or purplish, glabrous or pubescent, when immature dry and brittle, when mature the pericarp thin-membranous; seeds elongate, striate, the embryo green and clearly visible through the endosperm.

*Sphyrospermum* is a genus of about 22 species and ranges from southern Mexico through the highlands of Central America and the Andes of South America to Bolivia, east to French Guiana, and in the Caribbean from Haiti to Trinidad. Six species are currently known to occur in Costa Rica. *Sphyrospermum* is characterized by pedicels continuous with the calyx and usually thin and pendulous, terete calyces, usually small corollas, inferior ovary, thin-walled fruits, and seeds with green embryos. It is related to *Vaccinium* and *Dioegenesia* Sleumer, but details of the relationships are not as yet clear.

- 3b. Corolla 4–9 mm long ..... 5
- 4a. Corolla 2–2.3 mm long; leaf blades elliptic, ovate to lance-ovate; pedicels 7–15 mm long; calyx glabrous although minutely glandular-fimbriate with reddish fimbriae ..... *S. standleyi*
- 4b. Corolla 3–3.5 mm long; leaf blades suborbicular-elliptic or broadly subovate-elliptic to somewhat obovate; pedicels 5–9 mm long; calyx densely grayish pilose ..... *S. ellipticum*
- 5a. Leaf blades suborbicular to oblong-ovate, barely longer than broad, (0.7) 0.9–1.5 (1.8) cm long, the apex rounded or obtuse; flowers usually extending well beyond the leaves; corolla 4–6 mm long; stamens 4 ..... *S. buxifolium*
- 5b. Leaf blades ovate to ovate-lanceolate, usually conspicuously longer than broad, (1) 2–3.5 (5) cm long, the apex obtuse to acute, sometimes shortly and bluntly acuminate; flowers rarely extending beyond the leaves; corolla (4) 5–7 (9) mm long; stamens 4–5 or 8–10 ..... *S. cordifolium*

**Sphyrropermum buxifolium** Poepp. & Endl., Nov. Gen. Sp. Pl. 1: 4, pl. 8. 1835. *Sophoclesia cordifolia* Benth. var. *oophylla* Kuntze, Rev. Gen. Pl. 2:384. 1891. *Vaccinium pachycardium* Standl., Fieldiana, Bot. 18: 883. 1938. Illustrated: J. L. Luteyn, Fl. Ecuador 54, pl. 8. 1996. Figure 3.

Epiphytic or terrestrial **shrubs** mostly 15–40 cm tall; mature stems pendent to ascending, terete, slender, ribbed, glabrate; twigs subterete, striate and ribbed, moderately short-pilose with white hairs, glabrate. **Leaves** with petioles terete, rugose, sometimes striate, 1–2 mm long, puberulous to glabrate; leaf blades coriaceous, suborbicular to oblong-ovate, (7) 9–15 (18) mm long, 8–20 mm wide, base cordate or rounded, apex rounded or obtuse, sparsely and inconspicuously short-pilose on both surfaces, glabrate, also usually inconspicuously glandular-fimbriate beneath, often on both surfaces, obscurely 3 (5)-plinerved from base, midrib and lateral nerves usually weakly impressed above and raised beneath but obscure, reticulate veinlets usually totally obscure, rarely slightly raised on both surfaces when visible. **Inflorescences** axillary, flowers 1 (2), usually extending well beyond leaves; floral bract ovate, ca. 0.5 mm long, apex obtuse, pilose; pedicels subterete, gradually swollen apically, (5) 10–18 mm long, glabrous to sparingly pilose, sometimes scattered glandular-fimbriate; bracteoles nearly basal, linear-aristate, ca. 0.5 mm long, ciliate. **Flowers** 4-merous; calyx ca. 2–2.8 mm long, tube obconic to subglobose, 1–1.8 mm diam., pilose to glabrate, glandular-fimbriate, limb suberect, ca. 0.5–1 mm long, lobes apiculate, ca. 0.8 mm long, with a tuft of hairs at apex or glabrous, sinuses concave; **corolla** submembranous, cylindric-urceolate, terete, 4–6 mm long, 1.5–3 mm diam., sparsely pilose to glabrous, sometimes only tips of lobes pilose, also usually glandular-fimbriate, white to pinkish, lobes strongly reflexed, narrowly triangular, 0.8–1.3 mm long, apex obtuse; **stamens** 4, equal, slightly shorter than corolla, ca. 5.4–5.5 mm long; filaments seemingly callose-thickened at base, 1.8–3 mm long, sparsely pilose or glabrous; anthers 1.8–3.5 mm long, thecae smooth, ca. 1–1.5 mm long, rounded but sometimes minutely mucronate at base, tubules ca. 1.6–2.2 mm long, dehiscing by short clefts ca. 0.4 mm long. **Berry** globose, succulent, ca. (6) 10 mm diam., pilose or glabrous, translucent, whitish or with a violet or lavender tinge to purple.

*Sphyrropermum buxifolium* occurs in tropical and premontane wet forest and rain forest and montane and elfin forest, 100–1800 (2200) m elevation. It is distributed from Nicaragua south to Bolivia and east to French Guiana. In Costa Rica it is widespread in all the cordilleras. Flowering occurs in nearly every month; fruiting in February and May–December. **Common**.

*Sphyrropermum buxifolium* is characterized by its small, suborbicular to oblong-ovate leaf blades that are rounded or obtuse at the apex; 4-merous flowers borne on long petioles that usually extend well beyond the leaves; corollas only 4–6 mm long; and 4 stamens. It is morphologically very similar to *S. cordifolium*, with which eventually it may be shown to be conspecific. The main differences between the species are the usually smaller, suborbicular leaf blades of *S. buxifolium* that additionally are usually shorter than the flowering pedicels vs. the larger, ovate and usually subcordate leaf blades of *S. cordifolium* that usually are equal to or exceed the flowering pedicels.

**Sphyrropermum cordifolium** Benth., Pl. Hartw. 222. 1846. *Sophoclesia cordifolia* (Benth.) Klotzsch, Linnaea 24: 29. 1851. *Sophoclesia flaccida* Seem., Bot. Voy. Herald 164. 1854. *Sphyrropermum majus* Griseb., Fl. Brit. W.I. 143. 1859. *Sophoclesia major* (Griseb.) Benth. & Hook.f., Gen. Pl. 2: 576. 1876. *Sophoclesia cordifolia* (Benth.) Klotzsch var. *normalis* O. Kuntze, Rev. Gen. Pl. 2: 384. 1891. *Vaccinium valerii* Standl., Fieldiana, Bot. 18: 884. 1938. *Themistoclesia valerii* (Standl.) Sleumer, Bot. Jahrb. Syst. 71: 390. 1941. Illustration: R. L. Wilbur & J. L. Luteyn, Ann. Missouri Bot. Gard. 65: 122, fig. 16. 1978. Figures 2V, 3, and 5.

Terrestrial or epiphytic **shrubs** mostly 2–6 dm tall; mature stems pendent, arching, or scandent, subterete, striate, glabrate; twigs subterete, ribbed or striate, densely to moderately spreading puberulent, glabrate. **Leaves**

with petioles terete, rugose, 1–2 (3) mm long, glabrous to pilose; leaf blades ovate to ovate-lanceolate, (1) 2–3.5 (5) cm long, (0.8) 1.5–2.5 (3) cm wide, base rounded, subcordate or broadly obtuse, apex obtuse or rounded to acute, sometimes shortly but bluntly acuminate, moderately short-pilose with white hairs on both surfaces, glabrate, usually also appressed glandular-fimbriate beneath with fimbriae ca. 0.1 mm long, 3 (5)-plinerved from base, midrib and lateral nerves often impressed above (sometimes raised) and raised beneath, often all but midrib obscure beneath, reticulate veinlets usually slightly raised but obscure. **Inflorescences** axillary, flowers 1 (2), sometimes extending beyond leaves; floral bract ovate, ca. 0.3 mm long, apex obtuse, pilose; pedicels terete, (10) 15–25 mm long, pilose or glabrous, also often with inconspicuous, appressed, glandular fimbriae apically; bracteoles nearly basal, oblong-aristate, ca. 0.4 mm long, pilose. **Flowers** 4–5-merous; calyx ca. 3 mm long, usually moderately to densely spreading pilose, occasionally sparingly so or glabrous, usually also appressed glandular-fimbriate, tube subglobose or thickly fusiform to short-cylindric, 1–1.5 (2) mm long, limb cylindric-campanulate, erect, 1–1.6 mm long, lobes deltate, 0.5–0.8 mm long, apex acute, often with a tuft of hairs at the tip, sinuses rounded; **corolla** membranous, cylindric-urceolate, (4) 5–7 (9) mm long, 1.2–3 mm diam., white to bright red, glabrous or puberulous apically, sparsely and inconspicuously glandular-fimbriate apically, lobes spreading, narrowly triangular, ca. 0.6 mm long, acute; **stamens** usually either 4–5 or 8–10, slightly shorter than corolla, 6.5–8 mm long; filaments slender, 2–5 mm long, pilose or glabrous; anthers 2–4 mm long, thecae ca. 1–1.6 mm long, tubules ca. 1.5–2.3 mm long, dehiscent by clefts to 1.3 mm long. **Berry** globose to fusiform, to 15 mm diam., pilose or glabrous, translucent white or white with a violet tinge at maturity.

*Spherospermum cordifolium* is found in premontane and montane wet and rain forest to elfin forest, 100–2000 (2700) m elevation. It is distributed from southern Mexico, south to Bolivia, east to French Guiana, and onto the island of Hispaniola. In Costa Rica it is common throughout the cordilleras de Tilarán, Central, and Talamanca. Flowering occurs in nearly every month; fruiting in November–January and June–August. **Common.**

*Spherospermum cordifolium* is characterized by its ovate to ovate-lanceolate leaf blades that are usually conspicuously longer than broad with the apex obtuse to acute or sometimes shortly and bluntly acuminate and stamens 4–5 or 8–10. Usually it has pedicels about equaling the leaf length, and so the flowers easily stand out from the leaves that subtend them. Sometimes, however, leaves are much longer than the pedicels, so the flowers are overshadowed by the subtending leaves. Its relationship to *S. buxifolium* is mentioned under that taxon.

***Spherospermum dissimile*** (S. F. Blake) Luteyn,

Opera Bot. 92: 126. 1987a. *Vaccinium dissimile* S. F. Blake, J. Bot. 53: 271. 1915. *Disterigma dissimile* (S. F. Blake) S. F. Blake, Proc. Biol. Soc. Wash. 35: 120. 1922. Illustration: J. L. Luteyn, Fl. Ecuador 54, color plate 5. 1996. Figure 3.

Terrestrial, or more commonly, creeping epiphytic, viney **shrubs** interwoven amongst bryophytes along ground or high in trees; mature stems wiry, perhaps to 1 m long, 1–1.5 mm diam.; twigs densely spreading puberulent, glabrate. **Leaves** with petioles 1–2 mm long, puberulent; leaf blades coriaceous, ovate, lance-ovate or narrowly to broadly elliptic, 1–3 (4) cm long, 0.8–1.5 (2) cm wide, base rounded to cuneate, apex acute, glabrous above and beneath, also often sparsely to moderately appressed glandular-fimbriate beneath with fimbriae 0.1–0.2 mm long. **Inflorescences** axillary, flowers solitary; floral bract broadly reniform, ca. 0.3–0.4 mm long, apex rounded, glabrous; pedicels 1–2 (4) mm long, weakly hispidulous; bracteoles basal to medial, ovate to broadly oblong, apex obtuse to broadly rounded, 0.8–1 mm long, puberulent. **Flowers** 4-merous; calyx ca. 2.2–2.8 mm long, tube campanulate, 0.8–1.2 mm long, densely hirsutulous with hyaline to golden-yellowish hairs 0.1–0.2 mm long, limb erect-spreading, ca. 1.3 mm long, sparsely hirsutulous, lobes broadly deltate, 0.7–0.8 mm long, acute or obtuse, moderately to densely hirsutulous; **corolla** campanulate, 7–10 mm long, 6–9 mm diam., dark red or maroon, sparsely and inconspicuously glandular-fimbriate with fimbriae 0.1–0.2 mm long, lobes erect to spreading, deltate, 1.5–2 mm long, ca. 3.5 mm wide at base, acute; **stamens** 8, ca. 4.3–5.8 mm long, black to brownish-red; filaments 1.3–4 mm long, sparsely to densely pilose; anthers 2–3.3 mm long, thecae ca. 1.7 mm long, papillose, tubules 1.6–2.5 mm long, dehiscent by introrse clefts 0.5–0.7 mm long. **Berry** depressed-globose, bluntly quadrangular, 0.7–1 cm diam., translucent pearl-white.

*Spherospermum dissimile* occurs in tropical wet forest to premontane and montane cloud forest, 400–1900 m elevation. The species is geographically widespread from Costa Rica to Ecuador, but it is rarely collected and easily overlooked because it grows among mosses at ground level or high in the canopies of old, moss-covered trees and because of its dark, dull (not brightly colored) red corollas. In Costa Rica it is found in the Cordillera Central, especially along the Atlantic slopes. Flowering occurs in nearly every month; fruiting specimens have been collected only in July. **Rare/Infrequent.**

*Spherospermum dissimile* is characterized by its lianoid, thin-stemmed habit; short pedicels; and dark red, campanulate corollas. There has been much controversy over the generic placement of this species. Blake (1915) originally described it in *Vaccinium*, but he soon transferred it (without

comment) to *Disterigma* (Blake, 1922). A. C. Smith (1933), followed by Sleumer (1936), moved it back into *Vaccinium*, mainly because its pedicels and bracteoles were not of the "typical" *Disterigma* type. There it remained, although Wilbur and Luteyn (1978) stated that it did not "rest comfortably" in either genus. In 1982, Luteyn collected the first mature fruits in Ecuador and then again in Colombia in 1984, and in 1987 he transferred the species to *Sphyrospermum* based on the translucent, whitish, thin, membranous pericarp of the mature fruits and the green embryos in the mature seeds—characters that are used to distinguish the genus *Sphyrospermum* (see Luteyn, 1987a, for more details). [Note: R.L.W. favors continued placement of this species within *Vaccinium* as *V. dissimile*; J.L.L. maintains it in *Sphyrospermum* for the reasons given in the discussion above.] Plants of this species are said to be cultivated at "Lankester's Garden" (at Finca Silvestre, Cóncevas de Cartago).

***Sphyrospermum ellipticum*** Sleumer, Feddes Rept. Spec. Nov. Regni Veg. 41: 121. 1936. Figures 5 and 7.

Epiphytic **shrubs**; mature stems thin, elongate, terete, glabrous; twigs short-puberulent. **Leaves** with petioles ca. 2 mm long; leaf blades subcoriaceous, suborbicular-elliptic or broadly subovate-elliptic to somewhat obovate, (1.5) 2.8–6 cm long, 2.3–3 cm wide, base rounded or slightly cordate, apex rounded or nearly so, obscurely 3–5-plinerved from base, midrib and lateral nerves slightly raised beneath, reticulate veinlets obscure. **Inflorescences** axillary, flowers solitary; floral bract not seen; pedicels terete, striate, 5–9 mm long, sparsely short-pilose, glabrous; bracteoles nearly basal to located medially, aristate, 0.3–1 mm long. **Flowers** 4-merous; calyx ca. 2 mm long, tube subglobose, abruptly contracted at apex, ca. 2 mm diam., densely grayish pilose, limb campanulate, sparsely pilose, lobes deltate, ca. 0.4 mm long, acute, sparsely pilose, sinuses rounded; **corolla** subcylindric, somewhat inflated at middle, 3–3.5 mm long, ca. 1.5 mm diam., scattered short-pubescent and fimbriate, white to pink, lobes ca. 0.5 mm long; **stamens** 4, ca. 2.8 mm long; filaments ca. 1.6 mm long, subglabrous; anthers ca. 1.2 mm long, thecae ca. 0.6 mm long, tubules ca. 0.6 mm long. **Berry** spherical, pilose, ca. 10 mm diam., translucent white to lavender.

*Sphyrospermum ellipticum* is found in primary rain forest and cloud forest, 30–1000 m elevation. It is distributed from Costa Rica to Ecuador but is extremely rare and poorly collected. The only known collections of the species in Costa Rica include Parque Nacional Corcovado, *Kernan & Phillips 516*; Parque Nacional Guanacaste, Estación San Ramón, *Morales et al. 2545*; Osa Peninsula,

*Raven 21687*; Osa Peninsula, vic. Jalaca Station, *Allen 5307*; locality unknown, *McAlpin s.n.* Flowering specimens have been collected April–June; fruiting in April–August. **Endangered.**

*Sphyrospermum ellipticum* is characterized by its combination of usually elliptic leaf blades with rounded bases and apices, short pedicels, dense and grayish calyx pubescence, and short corollas. It is morphologically similar to and may be confused with *S. standleyi*; the differences between these two species are given in the key. Many more collections of both are needed in order to determine their circumscription and exact relationships.

***Sphyrospermum linearifolium*** Al. Rodr. & J. F. Morales in Morales & Rodríguez, Novon 15: 335, fig. 1. 2005.

Epiphytic, pendent **shrubs**; mature stems thin, glabrate, longitudinally striate; twigs reddish-brown to grayish-brown, shortly and sparsely puberulent. **Leaves** with petioles 1–2 mm long; leaf blades coriaceous to subcoriaceous, linear, usually revolute, 3.5–14.4 cm long, 0.2–0.8 cm wide, base narrowly obtuse, apex narrowly acute, glabrous above, shortly and sparsely glandular-fimbriate beneath, obscurely 2–3-plinerved, midrib sparsely pilose above. **Inflorescences** axillary, flowers solitary; floral bract not seen; pedicels 11–33 mm long, glabrous; bracteoles deciduous, linear, ca. 0.7 mm long. **Flowers** with calyx tube subglobose, terete to subterete, ca. 1.2 mm diam., glabrous, limb suberect, 0.8–1 mm long, lobes deltate, 0.2–0.6 mm long, acute, glabrous; **corolla** urceolate, ca. 5–6 mm long, ca. 3 mm diam., pink to whitish-pink, glabrous, lobes triangular, ca. 0.7 mm long, acute; **stamens** 5, slightly shorter than corolla; filaments ca. 1.8 mm long, glabrous to sparsely villose; anthers ca. 2.3 mm long, tubules dehiscing by oval pores. **Berry** spherical to subglobose, 5–8 mm diam., glabrous, whitish to whitish-maroon.

*Sphyrospermum linearifolium* is endemic to Costa Rica, where it has been collected on the Caribbean slopes of the Cordillera Central, at volcanoes Barva and Turrialba, 700–1500 m elevation. Only three collections are known: Limón: Altos de Pascua, cabeceras Quebrada Linda, 1 April 2001, *Morales 7823* and 11 July 2003, *Morales & Callejas 9426*, and Heredia: Parque Nacional Braulio Carrillo, falda Atlántica del Volcán Barva, 28 March 2002, *Morales 9772*. Flowering specimens have been collected in March and April; fruiting collections in March, April, and July. **Endangered.**

*Sphyrospermum linearifolium* is characterized by its linear leaves with a usually revolute margin. It is probably most closely related to *S. cordifolium* but is easily differentiated by leaf morphol-

ogy. More collections are needed of this rare and distinctive species. [The above description and discussion are based on the protologue; we have not seen the type collection]

**Spherospermum standleyi** A. C. Smith, Brittonia 1: 210. 1933. Figure 5.

Straggly, epiphytic or terrestrial **shrubs** 0.4–0.6 (1) m tall; mature stems subrugose, cinerous. **Leaves** with petioles subterete, 1.5–2 mm long; leaf blades subcoriaceous, the surfaces wrinkled, elliptic, ovate to lance-ovate, 2–6.5 cm long, 1.5–3 cm wide, base rounded or obtuse, apex obtuse, 3 (5)-plinerved, midrib impressed to plane (apically) above, lateral nerves impressed to plane but sometimes slightly raised apically, mostly obscure with only the inner 2 conspicuous above, reticulate veinlets obscure above, all nerves raised and conspicuous beneath. **Inflorescences** of axillary or ramiflorous, solitary or paired flowers; floral bract not seen; pedicels 7–15 mm long, swollen apically; bracteoles located along basal 1/3 of pedicel, subopposite, aristate, ca. 0.2–0.3 mm long. **Flowers** 4-merous; calyx 1–2.8 mm long, 1.5 mm diam., glabrous but minutely glandular-fimbriate with fimbriae 0.1 mm long, reddish, tube ca. 1–2 mm long, limb suberect, ca. 0.8 mm long, lobes apiculate, ca. 0.2 mm long; **corolla** cylindrical, 2–2.3 mm long, ca. 1 mm diam., white to pinkish, lobes deltate, acute, ca. 0.3 mm long; **stamens** 4, slightly shorter than corolla; filaments ca. 1.2 mm long; anthers ca. 1 mm long, tubules as long as thecae. **Berry** subglobose, 3–8 mm diam., translucent white.

*Spherospermum standleyi* is endemic to the premontane forest, 900–1500 m elevation in Costa Rica, from the Cordillera de Tilarán (at Monteverde, Alajuela Prov.) and the Cordillera de Talamanca (at Orosí, Cartago Prov. and in the Cantón de Talamanca, Limón Prov.). This species is known from only five collections and is poorly understood. It is not found in Panama as previously reported in the Flora of Panama (Wilbur & Luteyn, 1978: 124), the specimen cited there having been misidentified. Flowering and fruiting specimens have been collected in March and June only. **Endangered.**

*Spherospermum standleyi* is characterized by its small corolla (2–2.3 mm long), elliptic or ovate to lance-ovate leaf blades, pedicels that are 7–15 mm long, and glabrous calyx, although it may bear minute, reddish, glandular-fimbriae. The species' re-

lationships are obscure at this time, but it is probably related to *S. ellipticum* (see discussion above).

**Themistoclesia Klotzsch**

REFERENCE—J. L. Luteyn, New species, new records, and neotypification of some Mesoamerican Ericaceae. Brittonia 48: 241–249. 1996. [*Themistoclesia*, pp. 247–248]

Epiphytic **shrubs**. **Leaves** alternate, usually distichous, petiolate, the blades subcoriaceous to coriaceous, occasionally thick-fleshy, the margin entire, the venation obscurely plinerved or rarely pinnate. **Inflorescences** axillary, fasciculate, racemose or flowers solitary (in ours); pedicels continuous with calyx (possibly articulate in *T. alata*); bracteoles 2, basal, inconspicuous. **Flowers** (4) 5-merous, without odor; calyx synsepalous, tube obconic or short-cylindric, bluntly angled or rarely strongly winged, limb erect to slightly spreading, lobes minute to well developed; **corolla** sympetalous, aestivation valvate, ovoid to cylindric, terete or angled but not winged, the lobes usually apiculate, ca. 1/10–1/3 overall corolla length, not strongly reflexed; **stamens** 4–5 or 8–10, equal or alternately slightly unequal, equal to or more than 1/2 as long as corolla; filaments distinct; connectives lacking disintegration tissue or spurs; anthers lacking awns, thecae smooth, tubules 2 and distinct, or fused into 1 (*T. pentandra*), as wide as and nearly equal to or about two times longer than thecae, these smooth, dehiscent by short, introrse clefts or pores; pollen grains in tetrahedral tetrads, lacking viscin threads; ovary inferior; style filiform, included, glabrous. **Fruit** a berry; seeds covered by a translucent, mucilaginous sheath, the embryo green.

*Themistoclesia* is a genus of about 25 species distributed from Costa Rica to Bolivia. Four species are currently known to occur in Costa Rica. It is characterized by pedicels that are continuous with the calyx; an angled to rarely winged calyx; usually small and distichous leaves (in Costa Rica); terete and small corollas; dehiscence by short, terminal or oblique pores; seeds that are covered by a translucent, mucilaginous sheath; and green embryos. It is related to *Spherospermum* and *Diogenesia* Sleumer, but taxonomic revisions of all three genera are needed before their relationships can be clarified.

**Key to the Species of *Themistoclesia***

- 1a. Leaves spirally arranged along stems; leaf blades flat, apically acute to obtuse; calyx tube distinctly 4–5-winged; stamens 5 (6, 8 or 10); anther tubule 1 ..... *T. pentandra*

- 1b. Leaves distichously arranged along stems; leaf blades often concave, apically acute or acuminate; calyx tube bluntly 5-angled, not winged; stamens (8) 10; anther tubules 2 ..... 2
- 2a. Corolla 3–4.8 mm long; leaf blades less than 2 cm long, base narrowly obtuse to rounded, often appearing acute due to slightly involute margin ..... *T. smithiana*
- 2b. Corolla 5–7 mm long; leaf blades more than 2 cm long, base rounded, subtruncate or subcordate ..... 3
- 3a. Bracteoles ovate to hemispheric, completely concealing the glabrous pedicels; corolla cylindric, short-pilose throughout; stamens ca. 5 mm long, the filaments short-pilose, the thecae bearing finger-like appendage at base ..... *T. costaricensis*
- 3b. Bracteoles awl-shaped, never concealing the hispidulous pedicels; corolla urceolate, hispidulous apically; stamens 2.5–2.7 mm long, the filaments glabrous, the thecae lacking basal appendage ..  
..... *T. horquetensis*

***Themistoclesia costaricensis*** Luteyn & Wilbur,  
Brittonia 29: 265. 1977. Figure 5.

Pendent, epiphytic **shrubs**; mature stems to 0.5 m long, terete, minutely striate, tan to reddish-brown, hispidulous with reddish-brown trichomes 0.6–0.8 mm long, glabrate with age. **Leaves** distichous, with petioles subterete, densely puberulous to short-pilose, 1–1.5 mm long; leaf blades flat or often concave, ovate, (1.6) 2–2.5 cm long, (0.8) 1–2 cm wide, base rounded or subcordate, apex acute or short-acuminate, hispidulous above especially near margin, glabrous beneath, brown above and olive-green or light brown beneath, obscurely 5-plinerved, midrib slightly impressed basally, raised apically above, slightly impressed but inconspicuous beneath, lateral nerves and reticulate veinlets slightly raised but inconspicuous above, totally obscure beneath. **Inflorescences** axillary, flowers solitary, with 4, minute, basal bracts; floral bract ovate, ca. 1.5 mm long, ciliate; pedicels completely concealed by bracteoles, terete, 1–2 mm long, glabrous; bracteoles basal, ovate to hemispheric, ca. 1 mm long, apically hispidulous. **Flowers** 5-merous; calyx ca. 3.2–4 mm long, glaucous, copiously short-pilose with translucent or reddish tinged trichomes 1–1.2 mm long, tube obconic, bluntly 5-angled, ca. 3 mm long, limb 1–1.5 mm long, campanulate, lobes apiculate, obscure; **corolla** cylindric, narrowed at throat, 5–6.2 mm long, ca. 2.2 mm diam. near base, short-pilose throughout, white, lobes ca. 1 mm long; **stamens** 10, ca. 5 mm long, equal; filaments 2.8–3.2 mm long, short-pilose over entire length; anthers ca. 2.5–2.8 mm long, thecae ca. 1.2 mm long, with a minute, 0.1 mm long, finger-like appendage protruding from base, tubules 2, distinct, ca. 1.6 mm long, slightly longer than thecae, dehiscing by narrow clefts ca. 1.3 mm long; style 5–6 mm long. **Berry** spherical, ca. 9 mm diam., short-pilose, light bluish or lilac.

*Themistoclesia costaricensis* is found in premontane cloud forest, 1300–1850 m elevation, and is distributed in Costa Rica, adjacent Panama (Chiriquí Prov.), then again along the Panama/Columbia border region and from there south to central Colombia (Valle Dept.). In Costa Rica it is known only from the type locality: Cartago: property of ICE hydroelectric plant, 15–20 km beyond

suspension bridge over the Río Grande de Orosi, Luteyn et al. 4407. Flowering specimens have been collected in January, March, April, June, July, and December; fruiting in July (only known from one Panamanian collection). **Endangered.**

*Themistoclesia costaricensis* is characterized by its distichous leaves with flat or concave leaf blades that are greater than 2 cm long and have an acute or short-acuminate apex, bluntly 5-angled calyx, ovate to hemispheric bracteoles that completely conceal the glabrous pedicels, cylindric and short-pilose corollas, and 10 stamens with the filaments short-pilose and the thecae appendiculate at base. Morphologically, it is similar to *T. horquetensis*; the rather minor differences that distinguish the two are given in the key. Both species blend in well with their environment because of their straggly, wispy habit with few, solitary, tiny greenish-white flowers that are partially hidden by the leaves. Therefore, they are rarely noticed in the field and are poorly collected.

***Themistoclesia horquetensis*** Luteyn & Wilbur,  
Brittonia 29: 266. 1977.

Epiphytic **shrubs** ca. 5 cm tall; mature stems subterete or bluntly angled, minutely striate but becoming smooth, glaucous, pale reddish-brown, hispidulous with translucent trichomes 0.2–0.3 mm long, glabrous with age. **Leaves** distichous, with petioles subterete, flattened adaxially, 2–3 mm long, ca. 1 mm diam., hispidulous with translucent trichomes 0.2–0.3 mm long; leaf blades ovate, somewhat concave, (2.5) 3–4.5 cm long, 1.5–2.5 cm wide, base broadly rounded or subtruncate, sometimes involute, apex short-acuminate, apiculate, obscurely short-pilose above, especially near margin, glabrous beneath, 3 (5)-plinerved, nerves obscure, slightly impressed above, only midrib slightly raised beneath. **Inflorescences** axillary, flowers solitary (rarely 2), with 2–4, minute, basal bracts; floral bract ovate, 0.3–0.5 mm long, ciliate; pedicels angled, striate, glaucous, 1.5–2.5 mm long, hispidulous; bracteoles supramedial, awl-shaped, ca. 0.5 mm long, ciliate. **Flowers** 5-merous; ca-



lyx 3–4.3 mm long, glaucous, sparsely hispidulous with translucent hairs 0.2 mm long, tube obconic, bluntly 5-angled, 2–3 mm long, limb broadly campanulate, 1.5–1.7 mm long, lobes apiculate; **corolla** urceolate, strongly constricted at throat, 5–7 mm long, ca. 2.2 mm diam. near base, glabrous below but upper part of throat and lobes hispidulous, white to pale greenish-white, lobes ca. 0.5–1 mm long; **stamens** 10, ca. 2.5–2.7 mm long; filaments 1.5–2 mm long, glabrous; anthers 1–1.7 mm long inserted near base, thecae ca. 0.7–0.9 mm long, lacking basal appendages, tubules 2, distinct, ca. 0.8 mm long, equaling thecae, dehiscing by broad clefts ca. 0.7 mm long; style ca. 3.5 mm long. **Berry** ca. 5 mm diam.

*Themistoclesia horquetensis* is found in premontane cloud forest, 1200–2750 m elevation. It is endemic to Costa Rica and adjacent Panama (Chiriquí Prov.). In Costa Rica it has been collected only twice in Limón Province (Valle de Silencio, *Davidse et al.* 28705, and Caribbean slope between Río Terbi and Río Sini, *Davidse et al.* 29060). Flowering specimens have been collected in January–March, July, September, and December; fruiting in January. **Endangered.**

*Themistoclesia horquetensis* is characterized by its distichous leaves with blades that are greater than 2 cm long and with short-acuminate and apiculate apices, bluntly 5-angled clayx, awl-shaped bracteoles that never conceal the hispidulous pedicels, urceolate and apically hispidulous corollas, and 10 stamens with the glabrous filaments. Morphologically, it is similar to *T. costaricensis* and is discussed with that species.

**Themistoclesia pentandra** Sleumer, Bot. Jahrb. Syst. 71: 392. 1941. Figures 2S and 5.

Epiphytic, often slender and straggly **shrubs** 0.3–0.6 (1.5) m tall, arising from lignotubers; mature stems ascendent, terete, striate, fissured, grayish to brown or reddish-brown, moderately to densely spreading short-pubescent or short-pilose with hyaline trichomes 0.2–0.6 mm long, glabrate with age. **Leaves** spirally arranged, with petioles broadly canaliculate adaxially, (1.5) 2–4 mm long, short-pilose; leaf blades elliptic to oblong-elliptic, flat, (1.5) 2–3.5 (4.5) cm long, (0.8) 1.2–2 (2.5) cm wide, base cuneate, less commonly rounded, apex acute to obtuse, moderately but inconspicuously spreading short-pilose to puberulous on both surfaces when young but becoming glabrate or more sparsely pubescent, lower surface also inconspicuously moderately glandular-fimbriate and with 1–2 pairs of circular, concave, blackish glands ca. 0.2 mm diam. at base, obscurely 3–5-plinerved, midrib and lateral nerves slightly raised above and beneath, reticulate veins obscure on both surfaces. **Inflorescences** axillary, flowers solitary or rarely paired, with 2 or 4, minute, triangular bracts at base, <1.5 mm long; pedicels terete, 1.5–2.5 mm long, puberulous; bracteoles appressed, lanceolate, 1.2–1.5 mm long, puberulous. **Flowers** 4–5-merous; calyx 5–

mm long, tube 3.4–4 mm long, conspicuously 4–5-winged, sparingly to moderately beset with minute, glandular trichomes, the wings 1–2 mm wide, pale greenish, conspicuously ciliate with hyaline trichomes 0.2–0.4 mm long, these trichomes also occurring elsewhere on surface, limb 0.8–1 mm long, lobes minutely apiculate; **corolla** cylindric to somewhat cylindric-urceolate, narrowly winged over entire length, sharply quadrangular or pentagonal, 3–4.5 mm long, 2–2.5 mm diam. at base, moderately ciliate, broadened at base throughout both internally and externally, also bearing scattered, tiny glandular fimbriae, light salmon-orange to orangish-red with pale yellow to cream tips, lobes erect or slightly spreading and exposing tips of stamens, narrowly triangular, 1–1.5 mm long, acute, minutely mucronate; **stamens** 5 (6, 8, or 10), 3.2–3.5 mm long, equal or nearly so, about as long as corolla; filaments ca. 1.5 mm long, glabrous or sparingly ciliate, broadened at base, thecae 1–1.2 mm long, tubule 1, conical, 1.5–1.8 mm long, dehiscing by a single, oblique pore, ca. 0.8–1 mm long; stigma truncate; style 3–3.5 mm long, about as long as corolla. **Berry** ± ellipsoid-quadrangular, ca. 8 mm long, ca. 10 mm diam., violet to blue-black.

*Themistoclesia pentandra* is found in primary and premontane cloud forests, 700–1800 m elevation. It is endemic to Costa Rica and Panama. In Costa Rica, it has been collected fewer than 12 times, all from the Caribbean slopes of the cordilleras de Tilarán, Central, and Talamanca. Flowering specimens have been collected in January, March, April, and July; fruiting in March and April. **Rare/Infrequent.**

*Themistoclesia pentandra* is characterized by having leaves spirally arranged along the stems, leaf blade apices that are acute to obtuse, a strongly 4–5-winged calyx tube, 5 (6, 8, or 10) stamens, and a single anther tubule. While the original description and indeed the specific epithet indicate 5 stamens, most recent collections seen have 8 or 10, although many herbarium specimens lack corollas and stamens. It is possible that more than one species is included under this binomial. The interspecific relationships of *T. pentandra* are unclear at this time, although it is morphologically very similar to *T. alata* Luteyn, a species known from the Panama/Colombia border region to NW Ecuador. Both species have strongly winged calyx tubes and single anther tubules. *Themistoclesia alata* is itself an anomalous species in the genus, seemingly having the unique character of pedicels articulated with the calyces (Luteyn, 1996a).

**Themistoclesia smithiana** (Standl.) Sleumer, Bot. Jahrb. Syst. 71: 392. 1941. *Vaccinium smithianum* Standl., Fieldiana, Bot. 18: 833. 1938. Illustration: R. L. Wilbur & J. L. Luteyn, Ann.

Missouri Bot. Gard. 65: 129, fig. 17. 1978. Figures 2T and 3.

Pendent to spreading, epiphytic **shrubs** mostly 0.2–0.3 (0.5) m tall; mature stems terete, slender, brown or reddish-brown to grayish, densely to moderately short-pilose with hyaline trichomes 0.2–0.5 mm long, maturing to glabrate. **Leaves** distichous, with petioles terete, densely hispidulous, 0.5–1.5 mm long; leaf blades thickly coriaceous, concave, lanceolate, (7) 10–15 (18) mm long, (3) 6–8 mm wide, base narrowly obtuse to rounded, or sometimes strongly involute thus appearing acute, apex acute to acuminate, often deciduously apiculate, inconspicuously but copiously short-pilose above when young, becoming glabrate, trichomes slender, spreading, ca. 0.2 mm long, beneath glabrous except for reddish-brown, minute, glandular trichomes 0.1 mm long or less, venation obscure above except sunken midrib, completely obscured beneath. **Inflorescences** axillary, flowers solitary, with several basal bracts; floral bract ovate, ca. 0.8 mm long, short-pilose; pedicels terete, short-pilose, 1–1.2 mm long; bracteoles linear to linear-oblong, 0.4–0.6 mm long, reddish-brown, short-pilose. **Flowers** 5-merous; calyx ca. 5 mm long, copiously short-pilose with hyaline trichomes 0.3–0.6 mm long, tube obconic, terete, ca. 2.5–3 mm long, limb ca. 2 mm long, campanulate-rotate, lobes triangular, 1.2–1.5 mm long, conspicuous, acute to acuminate; **corolla** terete or obscurely 5-angled, urceolate, broadly ovoid, abruptly and conspicuously constricted at throat, 3–4.8 mm long, 2.5–3 mm diam. near base, 0.8–1 mm diam. at throat, glabrous in basal  $\frac{1}{3}$  but short-pilose apically, pale yellow to pale greenish-white or white, lobes linear-oblong, 0.5–0.8 mm long, strongly flaring and reflexed; **stamens** 8 or 10, equal, ca. 2.5–3.5 mm long; filaments slender, ca. 1.3–2 mm long, terete, glabrous, attached medially; anthers ca. 1.5–2 mm long, thecae 0.6–1 mm long, straight, tubules 2, 0.8–1.3 mm long, dehiscing by short, oval clefts ca. 0.6 mm long; style ca. 3 mm long. **Berry**  $\pm$  spherical, inconspicuously angled, 5–7 mm long, ca. 4 mm diam., bluish.

*Themistoclesia smithiana* is found in montane cloud forest, 1100–2000 m elevation. It is endemic to the cordilleras Central and Talamanca of Costa Rica and adjacent western Panama. Flowering specimens have been collected in December–January and July–August; fruiting in July and December. **Rare/Infrequent.**

*Themistoclesia smithiana* is characterized by its distichously arranged leaves with small (<2 cm long), concave blades that are narrow and involute at the base and acute or acuminate at the apex, bluntly 5-angled calyx tube, small (3–4.8 mm long) corolla that is sharply constricted at the throat, and 8 or 10 stamens. An unusual population exists in Limón Province (Parque Nacional Cordillera de Talamanca, Cantón de Talamanca, *Herrera 5915* and *5434*), which has very long and narrow, lanceolate, acuminate leaf blades 15–22

mm long and ca. 5 mm wide. The narrowness of the leaf blades is accentuated because the margin is strongly revolute over its entire length; all other features fall within the range of the species. The interspecific relationships of *T. smithiana* await a revision of the entire genus.

#### **Thibaudia** Ruiz & Pav. ex J. St.-Hil.

Terrestrial or epiphytic **shrubs**. **Leaves** alternate, petiolate, the blades coriaceous to subcoriaceous, the margin entire (in ours) or crenulate, the venation pinnate or plinerved (in ours). **Inflorescences** axillary or terminal, glomerulate, subfasciculate, racemose or paniculate (in ours), few- to many-flowered; floral bract small, inconspicuous; pedicels articulate with calyx (in ours) or rarely continuous; bracteoles 2, submedial. **Flowers** 5-merous; calyx synsepalous, tube short-cylindric or campanulate, occasionally narrowly 5-angled or winged, limb erect to slightly spreading apically; **corolla** sympetalous, aestivation valvate, subcylindric, occasionally 5-angulate, rarely weakly to strongly winged, rarely slightly zygomorphic, the lobes valvate; **stamens** 10, equal, often nearly as long as corolla; filaments equal, distinct or connate (in ours); connectives lacking disintegration tissue or spurs; anthers equal, lacking awns, thecae smooth or minutely papillate, tubules 2, distinct (in ours) or rarely partially connate, about as long and wide as thecae or rarely twice as long, dehiscing by elongate, introrse clefts; pollen grains in tetrahedral tetrads, lacking viscin threads; ovary inferior; style filiform. **Fruit** a berry; seeds numerous.

*Thibaudia* is a genus with about 70 species distributed from Honduras south to Bolivia and east to Suriname. One species occurs in Costa Rica. It is characterized by small floral bracts, pedicels usually articulate with the calyx, and stamens of similar morphology and equal in length with corolla. It is closely related to *Cavendishia* and perhaps *Anthopterus*.

**Thibaudia costaricensis** Hoerold, Bot. Jahrb. Syst. 42: 311. 1909. *Psammisia rhododelphis* K. Schum. ex Wercklé, Bol. Fomento Costa Rica 1: 934. 1911, nom. nud. Illustration: R. L. Wilbur & J. L. Luteyn, Ann. Missouri Bot. Gard. 65: 131, fig. 18. 1978. Figures 2P and 12.

Usually epiphytic **shrubs**; mature stems elongate to 2 m long, terete, cinereous, glabrous. **Leaves** with petioles glabrous, 2–3 (4) mm long; leaf blades chartaceous or thin-coriaceous, oblong, lanceolate-oblong to oblong-elliptic, (10) 12–24 cm long, (1.7) 3.5–5 (7.5) cm wide, base cuneate and often short-attenuate, apex caudate acuminate, apparently glabrous or with inconspicuous, glandular-fimbriate trichomes on both surfaces, 3–5-plinerved, lateral nerves originating near base, midrib and inner pair of laterals strong and conspicuous for entire length, midrib impressed above and prominently raised

beneath, reticulate veinlets slightly raised on both surfaces. **Inflorescences** axillary, ramiflorous, often at leafless nodes, usually on branches of previous season, usually paniculate, sometimes racemose then usually with 2–3 (6) racemes per node, 15–30-flowered, numerous; rachis slender, 2–5 cm long, laxly and sparsely puberulous or glabrous; floral bract deciduous, sometimes caducous, ovate to broadly ovate, 1–1.5 mm long, long-acuminate, margin fimbriate and sometimes also ciliate; pedicels articulate with calyx, subterete, glabrous or puberulous, 10–16 mm long, apically slightly swollen, pinkish to rose; bracteoles submedial, deciduous, ovate-lanceolate, 0.8–1.2 mm long, long-acuminate, margin fimbriate and sometimes also ciliate. **Flowers** with calyx ca. 3–4 mm long, tube campanulate, rugose, ca. 1.7–2 mm long, ca. 2.5 mm diam., sparsely puberulous or glabrous, pinkish to roseate, limb 1–2 mm long, erect or spreading, lobes 0.5–1 mm long, acute, sometimes cartilaginous; **corolla** actinomorphic, membranous, bistratose, cylindric, slightly contracted at base and throat, 9–10 mm long, 3–3.5 mm diam., translucent white, lobes 1–1.5 mm long; **stamens** ca. 7–9.2 mm long, equal or almost so; filaments membranous, firmly connate into a glabrous tube 2–3 mm long; anthers 5.5–7.2 mm long, thecae 2–3.5 mm long, tubules distinct, 3–3.7 mm long, dehiscing by elongate, oval clefts about  $\frac{1}{2}$  as long as tubule; stigma broadly peltate, ca. 1 mm diam.; style ca. 10–12 mm long, exserted 1–2 mm at maturity, glabrous. **Berry** spherical, 7–8 mm diam., blue-black.

*Thibaudia costaricensis* is found in cloud forest, 700–2200 m elevation. It is distributed in Honduras, Costa Rica, and western Panama (Chiriquí Prov.). Flowering specimens have been collected in February–June, October, and December; fruiting in May and June. **Widespread.**

*Thibaudia costaricensis* is characterized by its paniculate inflorescence (unique among Costa Rican ericads), long-lanceolate leaf blades, and small, translucent white corollas. This distinctive and relatively uniform species is the only representative of the genus in Central America. Sterile collections with long and narrow leaf blades may be confused with *Satyria warzsiwiczii*. *Thibaudia costaricensis* is morphologically most similar to *T. archeri* A. C. Smith (Colombia) and *T. albiflora* A. C. Smith (Ecuador), the three species having in common paniculate inflorescences; *T. costaricensis* has smaller leaves and corollas and less robust inflorescences.

## Utleya Wilbur & Luteyn in Luteyn & Wilbur

REFERENCE—J. L. Luteyn & R. L. Wilbur, New genera and species of Ericaceae (Vaccinieae) from

Costa Rica and Panama. *Brittonia* 29: 255–276, fig. 4. 1977. [*Utleya*, pp. 267–270]

Epiphytic **shrubs**; stems winged. **Leaves** alternate, petiolate, the blades coriaceous, the margin entire or crenate, the venation pinnate. **Inflorescences** axillary, racemose, few-flowered; floral bract small, inconspicuous; pedicels articulate with calyx; bracteoles 2, basal. **Flowers** 5-merous, without odor; calyx synsepalous, broadly and conspicuously 5-winged from base to apex, the wings alternating with lobes, tube obconic, limb erect, spreading; **corolla** sympetalous, aestivation valvate, urceolate, conspicuously 5-spurred, the spurs solid, arising from apical part of corolla tube, vertically oriented, opposite corolla lobes; **stamens** 10, equal, nearly as long as corolla; filaments distinct; connectives lacking disintegration tissue or spurs; anthers lacking awns, thecae slightly papillate, tubules distinct, about as wide as thecae, dehiscing introrsely although somewhat latrorsely by elongate clefts over entire length and somewhat onto theca; pollen grains in tetrahedral tetrads, lacking viscin threads; ovary inferior, 5-locular; style filiform; stigma truncate. **Fruit** unknown, but presumably a berry.

*Utleya* is a monotypic genus, endemic to central Costa Rica. It is characterized by having winged stems, pedicels articulate with the calyx, calyx wings that alternate with the lobes, fleshy corollas with spurs opposite the lobes, and stamens that dehisce by introrse or slightly latrorsely, oval slits that extend the entire length of the tubules and slightly onto the thecae. Its relationships are uncertain at this time but may lie with *Themistoclesia*, although in that genus the pedicels are continuous with the calyx; dehiscence is through terminal pores or short, oblique clefts; and the seeds are covered by a translucent, mucilaginous sheath. [Note: mature fruits are unknown in *Utleya*, although the immature seeds, at least, lack the mucilaginous sheath of *Themistoclesia*.] The nature of the corolla spurs in *Utleya* is of some interest; these spurs are very conspicuous, fleshy, and solid (not hollow) and are situated in the extreme apical part of the corolla opposite the lobes. Specimens of *Macleania pentaptera* Hoerold may sometimes bear apiculate spurs directly on the tip of the corolla lobes, but they are of a very different type and are in no way comparable to the pronounced spurs of *Utleya*.

*Utleya costaricensis* Wilbur & Luteyn in Luteyn & Wilbur, *Brittonia* 29: 267, fig. 4. 1977. Figures 2R and 10.

Epiphytic **shrubs** 1 m tall; mature stems glabrous, subterete and usually with narrow, corky wings; twigs glabrous, sharply angled, 3–5-winged with wings to 1 mm broad, reddish-brown; axillary buds with outer pair

of scales subulate, appearing stipular, 2–2.5 mm long. **Leaves** with petioles 4–12 mm long, sharply angled, canaliculate or carinate adaxially, carinate beneath, glabrous but with scattered glandular fimbriae; leaf blades broadly elliptic to ovate-elliptic, 2.5–5 (6) cm long, (1) 1.5–3.5 cm wide, base cuneate and decurrent onto petiole, apex short-acuminate, acute or obtuse, margin entire or apically crenate, glabrous on both sides but with scattered, reddish, glandular fimbriae, pinnately nerved, midrib very prominent above and raised in the basal  $\frac{1}{3}$ – $\frac{1}{2}$  but plane to slightly impressed apically, carinate beneath, secondary nerves arcuate and anastomosing near margin, slightly impressed above but raised beneath, reticulate veinlets slightly raised on both sides. **Inflorescences** racemose, 3–4 flowered; rachis glabrous, 3–6 mm long, sharply angled, with 2–4 tiny (<1 mm long), ovate bracts at base; floral bract ovate, ca. 1 mm long; pedicels subterete, striate, angled, 12–14 mm long, ca. 0.5 mm diam., glabrous but with scattered glandular fimbriae; bracteoles ovate, 1–1.5 mm long, apex acute, margin glandular-fimbriate. **Flowers** with calyx 5.5–8 mm long, 7–9 mm wide across apical tip including wings, broadly 5-winged, the wings 2–3 mm wide, alternate with and produced beyond lobes, glabrous but glandular-fimbriate at base, tube obconic and 2–2.5 mm long, limb spreading and ca. 2 mm long, lobes ca. 0.5 mm long, apiculate; **corolla** fleshy, urceolate, strongly constricted at throat, pentagonal, ca. 4 mm long, ca. 6 mm diam. including spurs, light pink, glabrous externally but densely pilose internally at throat, the spurs ovate-obtuse, laterally compressed, about twice as long as lobes, ca. 1.5 mm broad at widest point, the lobes slightly reflexed at anthesis, triangular, ca. 1 mm long, white; **stamens** ca. 3 mm long; filaments distinct, ca. 2 mm long, densely long-pilose in apical  $\frac{1}{2}$ ; anthers ca. 1.5–1.8 mm long, thecae strongly incurved at base, ca. 1 mm long, tubules ca. 0.5–0.75 mm long; style ca. 2 mm long, included, glabrous. **Berry** not seen.

*Uleya costaricensis* is endemic to the premontane forest, 1500–1800 m elevation. It is known only from the Caribbean slope of central Costa Rica (Cartago Prov., Orosi), from which it has been collected fewer than 12 times. Flowering specimens have been collected in May–July and December; mature fruits are unknown. **Rare/Infrequent.**

## Vaccinium Linnaeus

REFERENCES—H. O. Sleumer, Die Arten der Gattung *Vaccinium* L. in Zentral- und Sudameri-

ka. Notizbl. Bot. Gart. Berlin-Dahlem 13: 111–140. 1936. S. P. Vander Kloet, J. L. Baltzer, J. H. Appleby, R. C. Evans, & D. T. Stewart, A re-examination of the taxonomic boundaries of *Symphysia* (Ericaceae). Taxon 53: 91–98. 2004.

**Shrubs** or rarely **trees**, often rhizomatous; axillary buds with outer pair of scales sometimes elongate and appearing stipular. **Leaves** alternate to pseudo-opposite, persistent, petiolate, the blades with margin entire or serrate, the venation pinnate or plinerved. **Inflorescences** axillary, racemose, or rarely 1–2-flowered; pedicels articulate (in ours) or rarely continuous with calyx; bracteoles 2, basal. **Flowers** 4–5-merous, without odor; calyx synsepalous, tube cylindric to globose, lobes rarely obsolete; **corolla** sympetalous, aestivation imbricate or valvate, cylindric, urceolate, or campanulate, white to pink, greenish, or yellowish-green; **stamens** 8 or 10, equal, about equaling corolla; filaments equal, distinct or weakly connate at base, equal to or longer or shorter than anthers; connectives lacking disintegration tissue, with or without spurs; anthers equal, lacking awns, thecae smooth or minutely papillate, tubules 2, distinct, about as wide as thecae, dehiscing introrsely (sometimes obliquely), latrorsely, or terminally by pores or clefts; pollen grains in tetrahedral tetrads, lacking viscin strands; ovary inferior, 4–5 (falsely 10)-locular; style filiform, included and about as long as corolla, or rarely slightly exserted, glabrous; stigma small, simple or somewhat capitate. **Fruit** a spherical berry, crowned by the persistent calyx lobes and capped by the conspicuous nectariferous disc; seeds numerous, sometimes with mucilaginous sheath.

*Vaccinium* is a genus with approximately 450 species distributed in the Northern Hemisphere, Mesoamerica, the West Indies, South America, East Africa and Madagascar, Malesia, and Pacifica. Ten species are known from or are to be expected in Costa Rica. In Costa Rica, the genus is characterized by having pedicels articulate with the calyx, corollas of united petals, stamens of equal morphology and about equaling the corolla in length, inferior and 4–5 (sometimes falsely 10)-locular ovaries, and baccate fruit. *Vaccinium* is morphologically heterogeneous and not monophyletic. In Latin America, *Vaccinium* is morphologically most similar to *Disterigma*, the two being easily distinguished by the lack of calyx-clasping bracteoles at the apex of the pedicels in *Vaccinium*, although see Vander Kloet (1985) and Vander Kloet et al. (2004) for a different opinion.

## Key to Species of *Vaccinium*

- 1a. Leaf blades with (indistinctly) crenate to crenate-serrate margins, 1–4.7 cm long, (0.3) 1–2 (2.3) cm wide; corolla white to pinkish or red, membranous, unistratose, the aestivation imbricate 2
- 1b. Leaf blades with margins entire, (2) 3–8 (20) cm long, (0.8) 1–5 (8.5) cm wide; corolla usually

- yellowish- to creamy-green (rarely suffused with purplish), fleshy (membranous in *V. almedae*), bistratose, the aestivation valvate ..... 4
- 2a. Anther connectives spurred ..... *V. consanguineum*
- 2b. Anther connectives lacking spurs ..... 3
- 3a. Corolla appressed- to spreading-puberulous externally and moderately to densely pilose internally; pedicels 6–10 mm long; berry pilose, not glaucous ..... *V. talamancense*
- 3b. Corolla glabrous; pedicels 3–4 (6) mm long; berry glabrous, sometimes glaucous ..... *V. floribundum*
- 4a. Calyx limb with 5 saccate spurs opposite and at base of each calyx lobe ..... *V. luteynii*
- 4b. Calyx limb terete and lacking spurs ..... 5
- 5a. Calyx (4) 7–16 mm long, the tube always shorter than the limb, calyx lobes (1.8) 2–5 (6) mm long ..... 6
- 5b. Calyx 2–4.5 mm long, the tube longer than the limb, except *V. furfuraceum*, calyx lobes <1.5 mm long ..... 9
- 6a. Leaf blades conspicuously bullate, the base  $\pm$  clasping, the apex rounded; corolla cylindric-urceolate, proportionally less prominent than calyx ..... *V. bocatorensis*
- 6b. Leaf blades flat (sometimes weakly bullate in *V. jefense*, sometimes concave in *V. monteverdense*), the base not clasping, the apex acute to acuminate; corolla broadly cylindric to cylindric-campanulate, proportionally more prominent than calyx ..... 7
- 7a. Corolla 7–10 mm long, internally densely floccose; calyx lobes smooth; anther tubules ca. 1 mm long, glabrous, dehiscing introrsely to terminal ..... *V. floccosum*
- 7b. Corolla 10–18 mm long, internally glabrous; calyx lobes conspicuously striate; anther tubules ca. 3.5–5 mm long, long-pilose along inner surfaces, dehiscing latrorsely ..... 8
- 8a. Leaf blades often slightly concave, (2.4) 3.4–5.2 (8) cm long, the venation relatively inconspicuous; bracteoles 0.8–1.5 mm long; corolla 13–18 mm long, glabrous ..... *V. monteverdense*
- 8b. Leaf blades flat but often bullate, (4.5) 8–12 (20) cm long, the venation strong, conspicuous; bracteoles 5–8 mm long; corolla 10–13.5 mm long, hirsute and glandular-fimbriate externally especially on surface of lobes ..... *V. jefense*
- 9a. Corolla cylindric to urceolate, 5–8 mm long; staminal filaments about equaling or slightly shorter than anthers, the anther tubules <2 mm long ..... 10
- 9b. Corolla cylindric, cylindric-campanulate, to cylindric-funnelform, (5) 8–12 mm long (if corolla <8 mm long then color white and the mouth flaring to ca. 5 mm diam., *V. almedae*); staminal filaments conspicuously shorter than anthers, the anther tubules 3 mm long or longer ..... 11
- 10a. Leaf blades acute to rounded at base; calyx lobes 1.2–1.8 (2) mm long ..... *V. costaricensis*
- 10b. Leaf blades rounded to more typically cordate and amplexicaul at base; calyx lobes 0.5–1.2 mm long ..... *V. orosiense*
- 11a. Petioles 7–15 mm long; axillary buds with outer pair of scales long- aristate, to 10 mm long; corolla narrowly cylindric to cylindric- campanulate, glabrous, pale green to white, 5–9 mm long, 5–6 mm diam.; anther tubules dehiscing by truncate, terminal pores ..... *V. almedae*
- 11b. Petioles 1–4 mm long; axillary buds with outer pair of scales narrowly lanceolate, to 4.5 mm long; corolla broadly cylindric to cylindric-campanulate, glabrous to densely scurfily glandular-squamosely externally, green to pale yellowish-green or brownish-lilac (fide label) in *V. furfuraceum*, 8–12 mm long, 6–10 mm diam.; anther tubules dehiscing by introrse pores or latrorsely ..... 12
- 12a. Leaves and floral parts generally densely fimbriate; leaf blades bullate, basally rounded, the reticulate veinlets conspicuously raised beneath; corolla squamosely glandular-fimbriate externally; stamens dehiscing by latrorsely clefts, the tubules short-pilose along inner surfaces, not much longer than thecae ..... *V. furfuraceum*
- 12b. Leaves and floral parts without fimbriae, but leaf blades moderately fimbriate especially beneath; leaf blades flat, basally acute, broadly cuneate or acuminate, the reticulate veinlets usually obscure beneath; corolla essentially glabrous; stamens dehiscing by introrse pores, the tubules glabrous, conspicuously longer than thecae ..... *V. poasanum*

**Vaccinium almedae** Wilbur & Luteyn, Sida 21(3): 1607, fig. 1. 2005.

Epiphytic **shrubs** 1–2 m tall; mature stems terete, striate, dull to nitid, glabrous; twigs subterete to complanate, bluntly angled to furrowed, glabrous; axillary buds with outer pair of scales subulate, long-aristate to 10 mm long, appearing stipular. **Leaves** with petioles flattened or shallowly canaliculate adaxially, rugose, 7–15 mm long, 2–3.5 mm diam., glabrous; leaf blades coriaceous, elliptic, 6–18 cm long, 3–7.5 (9) cm wide, base rounded to short-acuminate, sometimes appearing involute in basal ½ cm, apex acute to acuminate, margin entire, glabrous on both surfaces, 3–5-plinerved, midvein raised in basal ⅓–½ then slightly impressed apically above, lateral nerves ± impressed above but raised beneath, reticulate veinlets slightly impressed above and raised beneath but there indistinct. **Inflorescences** axillary or ramiflorous, fasciculate to very short-racemose, (2) 4–10-flowered, when ramiflorous the inflorescence apparently usually subtended by a narrowly ovate, acuminate bract to 8 mm long; rachis (when present) to ca. 2 mm long, congested; floral bract small, ovate, 0.6–1.5 mm long, apex long-acuminate, margin ciliate and glandular-fimbriate; pedicels slender, 5–10 mm long, 0.2–0.3 mm diam., glabrous; bracteoles basal, ovate-deltate, 0.5–0.8 mm long, apex long-acuminate, margin ciliate and glandular-fimbriate. **Flowers** 5-merous; calyx ca. 3–4 mm long, glabrous, tube cylindric-obconic, ca. 1.5–2.2 mm long, limb thin, broadly flaring to rotate, often reflexed at anthesis, 1.5–1.8 mm long, lobes minute, ca. 0.2–0.4 mm long, sinuses flat to concave; **corolla** aestivation apparently valvate, membranous, thinly bistratose, often inflating in bud, apparently cylindric to cylindric-campanulate at anthesis, 5–9 mm long, 2.5–4 mm wide at base but broadening apically to ca. 5–6 mm diam., glabrous both externally and internally, pale green to white with lobes bordered red (hide label), lobes narrowly triangular to deltate, ca. 2.5 mm long, apex acute; **stamens** 10, 7–8 mm long; filaments 1–2.5 mm long, distinct (possibly united in basal 0.5 mm), ciliate, conspicuously shorter than anthers; connectives lacking spurs, glabrous; anthers 6–7 mm long, thecae ca. 1.4–2.2 mm long, incurved and apiculate at extreme base only, tubules distinct, ca. 3–4.8 mm long, glabrous, dehiscent by truncate to slightly flaring, terminal pores; style slightly exerted. **Berry** immature, 3–4 mm diam., glabrous.

*Vaccinium almedae* is known from three collections made in premontane, wet forest near the Fortuna Dam and Cerro Colorado sites in Chiriquí Province, Panama, 1150–1500 m elevation. It has not yet been collected in Costa Rica. Flowering specimens have been collected in January; immature fruits in late January and April. **Endangered.**

*Vaccinium almedae* is characterized by its long-aristate, axillary bud scales that appear stipular; short-racemose to fasciculate inflorescences that are sometimes ramiflorous, rotate to flaring calyx limb; minute calyx lobes; pale green to white corolla; staminal filaments that are conspicuously

shorter than the anthers; and anther tubules that are conspicuously longer than the thecae and that dehisce by truncate to slightly flaring, terminal pores. Its relationships are unclear at this time.

**Vaccinium bocatorensis** Wilbur, Sida 11: 441. 1986 [as *bocatorensis*].

Epiphytic, scandent **treelet**; mature stems ± terete, furrowed, epidermis cracking longitudinally; axillary buds with outer pair of scales narrowly lanceolate, 7–9 mm long, abruptly long-acuminate, appearing stipular. **Leaves** apparently subopposite, with petioles thick, stout, rugose, 2–3 mm long, 3–4 mm diam., short-puberulent adaxially, ± glabrous abaxially; leaf blades coriaceous, ovate to ovate-elliptic, 4–6.5 cm long, 3.5–5 cm wide, base rounded and slightly cordate, often somewhat clasping, apex ± rounded, margin entire, glabrous above and moderately but inconspicuously erect-short-pilose beneath with widely spaced, slender, hyaline trichomes 0.2–0.3 mm long, apparently lacking glandular fimbriae, 5 (7)-plinerved with 2–3 pairs of lateral nerves arising within 5–10 mm of base, midrib and lateral nerves impressed above and raised beneath, reticulate veinlets obscure. **Inflorescences** congregated apically and sometimes appearing terminal, racemose to subcorymbose, 6–12-flowered; rachis 2–5 cm long, ± terete, moderately and inconspicuously short-pilose; floral bract persistent, lanceolate to lance-ovate, 3–6 mm long, apex acute to acuminate, sparingly puberulent to short-pilose externally; pedicels terete, striate, 10–15 (20) mm long, ca. 1 mm diam., eglandular, moderately to densely puberulent with erect hyaline trichomes; bracteoles borne in basal ⅓, lanceolate to lance-oblong, 4–6 mm long, 0.6–1.5 (1.8) mm wide, adaxially glabrous and abaxially sparingly puberulent to short-pilose, margin ciliate. **Flowers** 5-merous; calyx rugose, 7–10 mm long, moderately to densely white-puberulent with erect hyaline trichomes and also inconspicuously and moderately ferrugineous, glandular-fimbriate, “purplish-red,” tube broadly cylindric, 3.5–4 mm long, fimbriate and glandular-pustulate throughout, limb cylindric-campanulate, 4.5–5.5 mm long, smooth, lobes narrowly triangular to lanceolate, 4–5 mm long, ca. 2–3 mm wide at base, acute, spreading-recurved or reflexed; **corolla** aestivation valvate, thick and fleshy, bistratose, urceolate to cylindric-urceolate, constricted at throat, 7–9 mm long, 6–7 mm diam., externally glabrous, internally glabrous or nearly so in basal half but increasingly tangled white-pilose apically, lobes broadly deltoid, ca. 2–2.5 mm long, ca. 2.5 mm wide at base, livid red (hide label) externally, exceedingly densely matted-tomentose internally; **stamens** 10, ca. 5–6.2 mm long; filaments weakly connate at base, ca. 2.5–3 mm long, ca. 0.5 mm wide at middle, moderately to densely sericeous at margin and on both surfaces especially on connective abaxially, slightly shorter than anthers; connectives lacking spurs; anthers ca. 3–4 mm long, thecae ca. 2.5 mm long, strongly incurved at base, tubules distinct, 1–1.5 mm long, glabrous, dehiscent by obliquely introrse pores; style included, ca. 7 mm long. **Berry** not seen.

*Vaccinium bocatorensis* is known only from the

type collection made in Bocas del Toro Province, Panama, along the heavily forested headwaters of the Río Colubre, near the Costa Rica border, 2400–2550 m elevation (L. D. Gómez *et al.* 22368, DUKE, MO). It has not yet been collected within the political boundaries of Costa Rica. The type collection was flowering in March 1984; fruits are unknown. **Endangered.**

*Vaccinium bocatorensis* is characterized by its subopposite leaves with stout, rugose petioles, bullate leaf blades with the apices rounded and the bases rounded to subcordate and often somewhat clasping; plinerved venation with the reticulate veinlets obscure beneath; elongate calyx with proportionately long lobes; thick and fleshy corolla that is urceolate to cylindric-urceolate and conspicuously constricted at the throat; and stamens with introrse dehiscence and glabrous tubules. The corolla is proportionally small and inconspicuous with respect to the calyx. *Vaccinium bocatorensis* keys closest to *V. floccosum* and *V. monteverdensis* because of their long calyces and calyx lobes, but its overall relationships within the genus are uncertain. The type collection was visited by *Bombus ephippiatus* (fide label data).

***Vaccinium consanguineum*** Klotzsch, Linnaea 24: 64. 1861. *V. irazuense* Sleumer, Notizbl. Bot. Gart. Berlin-Dahlem 12: 138. 1934. *V. consanguineum* Klotzsch var. *irazuense* (Sleumer) Sleumer Notizbl. Bot. Gart. Berlin-Dahlem 13: 126. 1936. Figures 2W, 4, and 8.

**Shrubs** or small **trees** (0.2) 1–3 (10) m tall; mature stems often compact and densely bushy, stiff, rigid, glabrous to densely puberulent, the bole (when present) up to 30 cm dbh; axillary buds with outer pair of scales broadly ovate, 1.2–2.5 mm long, apex acute to obtuse, glabrous to short-pilose, ciliate, inconspicuous, not appearing stipular. **Leaves** with petioles 1.5–3 mm long, often broadly canalliculate adaxially, glabrous or puberulent; leaf blades narrowly to broadly elliptic, occasionally oblong, (1) 1.5–3 (5.5) cm long, 0.5–1.2 (2) cm wide, usually 2–3 times as long as wide, base acute, apex usually tapering and acute, margin conspicuously callose-thickened and lighter in color than blade proper, shallowly serrulate with teeth mostly (1) 2–4 mm apart, each tooth often tipped with a darkish, glandular callosity, glabrous or with scattered glandular trichomes beneath and moderately puberulous along midrib, often with bluish tint, pinnately nerved with 4–7 secondary nerves per side, all nerves slightly raised on both surfaces and lighter color than blade proper, secondary nerves and reticulate veinlets often inconspicuous above but usually conspicuous beneath. **Inflorescences** racemose, 5–10-flowered; rachis sharply angled, 1–4 cm long, puberulent; floral bract ovate to oblong, 2–5 mm long, scarious, slightly puberulent or ciliate; pedicels 1–

2 mm long, puberulent; bracteoles subopposite, ovate to oblong, 1.5–3 mm long, scarious, ciliate but otherwise glabrous, entire to sparingly irregularly and minutely toothed. **Flowers** 4-merous; calyx glabrous, 3–4 mm long, tube campanulate, 1–2.3 mm long, limb 1.3–2.2 mm long, smooth, lobes deltate to broadly ovate, 0.8–1.5 mm long, apex acute to acuminate, ciliate but otherwise glabrous; **corolla** aestivation imbricate, membranous, unistratose, cylindric, 5–7.5 mm long, 2.7–4.5 mm diam., glabrous, creamy white with tinges of red or pink, lobes oblong, 1–1.7 mm long; **stamens** 8, 4.4–5.7 mm long; filaments distinct, 3–4 mm long, ciliate to pilose; connectives 2-spurred, the spurs originating near apical tip, ascendent, 0.2–0.6 (1) mm long, rarely vestigial; anthers 2.8–4 mm long, thecae 1.5–1.8 mm long, tubules distinct, 1.2–2 mm long, glabrous, dehiscing by introrse clefts 0.5–0.7 mm long; style included. **Berry** 5–6 mm diam., reddish to blue-black, often glaucous.

*Vaccinium consanguineum* is found in montane cloud forest, primary *Quercus* forest and open páramo with *Chusquea*, often rooted in ash near volcanic summits, and bogs, (1300) 1650–3400 (3800) m elevation. It is endemic to Costa Rica and adjacent western Panama. In Costa Rica, it occurs as both a shrub and a tree. [Note: This species was included by Standley (1920–1926, pp. 1101–1102) as a member of the woody flora of Mexico, but its presence north of Costa Rica was questioned by Sleumer (1936), and the species was not included by Standley and Williams (1966) in the *Flora of Guatemala*. The species is known to us only from the mountains of Costa Rica and western Panama.] Flowering and fruiting occur throughout the year, with the preponderance of flowering between January and July. **Common.**

*Vaccinium consanguineum* is characterized by its pinnately nerved and serrulate-margined leaf blades, racemose inflorescences with small white to pink flowers, spurred connectives (these rarely vestigial), and glaucous berries. The species varies from small, densely branched shrubs to large trees to 10 m tall. Leaf size also varies greatly with trees often having leaves at the higher end of the range. The small-leaved populations of *V. consanguineum* look especially like *V. floribundum*. Both species have spurred (or vestigially spurred) anthers, although the Costa Rican populations of *V. floribundum* lack spurs. Nevertheless, *V. floribundum* would appear to be its closest relative. The species is visited by bees (pers. observ.). The fruits may be sweet, with good flavor (seemingly the blue-black ones), or more tart and used to make jams (seemingly the red-fruited ones). Common names in Costa Rica include *arrayán* (*arrallan*) and *madroño*.



**Vaccinium costaricense** Wilbur & Luteyn in Luteyn & Wilbur, *Brittonia* 29: 270, fig. 5. 1977. *Symphysia costaricensis* (Wilbur & Luteyn) vander Kloet, *Taxon* 53: 97. 2004. Figures 6 and 8.

Terrestrial or epiphytic **shrubs** 1–3 (4) m tall; mature stems grayish to reddish-brown, glabrous; axillary buds with outer pair of scales sometimes narrowly lanceolate, to ca. 4 mm long, abruptly long-acuminate, appearing stipular. **Leaves** with petioles 1–2 mm long, glabrous; leaf blades coriaceous, sometimes slightly bullate, ovate or lanceolate to elliptic, (2.5) 4–8 (11) cm long, (1.5) 2.5–4.5 (6.2) cm wide, base acutely tapering to rounded, rarely narrowly auriculate, apex acute to shortly and bluntly acuminate, margin entire, slightly thickened and perhaps appearing slightly revolute, glabrous but moderately and inconspicuously appressed glandular-fimbriate on both surfaces, 3–5 (7)-plinerved and also somewhat weakly arcuately veined, basal part of midrib as well as lamina around base colored reddish when fresh and reddish-brown when dry, inner lateral nerves arising in basal 2 cm, midrib thickened and raised above in basal 2 cm then slightly impressed apically, lateral nerves slightly impressed above, reticulate veinlets slightly raised above, all nerves raised beneath but the reticulate veinlets often inconspicuous. **Inflorescences** often superficially appearing terminal, in umbelliform racemes, 10–15-flowered; rachis 1–2.5 (3) cm long, glabrous to sparingly and minutely puberulent; floral bract persistent, scale-like, ovate-lanceolate, lanceolate or triangular, 1–3.5 mm long, apex long-acuminate, glabrous to puberulent, minutely ciliate; pedicels 10–30 mm long, glabrous to inconspicuously puberulous, often also glandular-fimbriate with trichomes ca. 0.1 mm long at articulation; bracteoles located along lower  $\frac{1}{3}$  of pedicel, subopposite, appressed, persistent, lance-ovate to lanceolate, 0.8–3 mm long, glabrous to indistinctly ciliate. **Flowers** 5-merous; calyx 3.5–5 (5.8) mm long, glabrous to densely, minutely puberulent, tube campanulate, narrowed and rounded at base, ca. 2–2.5 (4) mm long, limb spreading-campanulate, equal to or more typically shorter than tube, 1.5–2 (2.5) mm long, smooth, lobes triangular, 1.2–1.8 (2) mm long, apex acute, sinuses rounded to obtuse at anthesis but often tearing and then appearing acute; **corolla** aestivation valvate, fleshy, bistratose, broadly cylindric to somewhat urceolate, 5–8 mm long and 4–7 mm diam. (ca. 8 mm long and 9 mm diam. when fresh), pale greenish-yellow, externally glabrous and internally moderately to densely pilose especially in throat and on lobes with whitish trichomes, lobes erect to spreading or somewhat reflexed, triangular, acute, 1–2 mm long; **stamens** 10, ca. 6 mm long; filaments 3–4 mm long, slightly adherent to base of corolla tube, ciliate to short-pilose; connectives short-pilose, lacking spurs; anthers ca. 3–4 mm long, thecae ca. 1.8–2 mm long, markedly incurved and apiculate at base, tubules distinct, 1–2 mm long, glabrous, dehiscent by introrse, slightly oblique or slightly flaring, terminal pores; style about equalling corolla, included or slightly exserted. **Berry** spherical, 11–16 mm diam., dark maroon to blackish-maroon, or purple.

*Vaccinium costaricense* grows in premontane

cloud forest, (700) 1480–2000 m elevation. It is found on the Caribbean watershed of the central volcanic cordillera between the northeastern slopes of Volcán Barva (Heredia Prov.) and the northwestern slopes of Volcán Irazú (San José Prov.) in Costa Rica and Bocas del Toro and Chiriquí provinces in western Panama. Flowering specimens have been collected in December and March; fruiting in March, July, and December. **Rare/Infrequent.**

*Vaccinium costaricense* is characterized by its combination of acutely tapering to rounded leaf blade bases, a calyx tube that is longer than the limb, corollas that are pilose internally at the throat, and short anther tubules. There is some notable morphological variation: nearly all the plants from intermediate elevations (1480–2000 m) of the Cordillera Central of Costa Rica have calyces densely puberulent, whereas all specimens from lower elevations (700–800 m) are glabrous. The plants from the Fortuna Dam region of Chiriquí Province, Panama, have leaf blades often basally acutely tapering and calyces always glabrous. Two collections from the Central Cordillera (Heredia Prov., Boyle *et al.* 1095, Wilbur & Luteyn 18576) have leaf blades narrowly auriculate, as is also seen in two collections of *V. poasanum* mentioned below. *Vaccinium costaricense* has a longer rachis; shorter calyx limb and lobes; smooth, not striate, calyx limb and lobes; and longer anther tubules than its morphologically closest relative *V. floccosum*, from western Chiriquí Province, Panama. These differences in the calyx may be influenced by where and how the plants grow, that is, epiphytes in the closed forest vs. terrestrial in exposed, windswept areas (pers. observ.). *Vaccinium costaricense* differs from *V. orosiense* by acutely tapering to rounded leaf blade bases (not cordate and amplexicaul) and shorter calyx lobes (at least in the Costa Rican populations). The characters that distinguish these three species of *Vaccinium* are admittedly few, and more collections are needed to help clarify their morphologies and relationships.

**Vaccinium floccosum** (L. O. Williams) Wilbur & Luteyn in Luteyn & Wilbur, *Brittonia* 29: 272. 1977. *Hornemannia floccosa* L. O. Williams, *Brittonia* 18: 248. 1966. *Symphysia floccosa* (L. O. Williams) L. O. Williams, *Phytologia* 24: 158. 1972.

Terrestrial or epiphytic **shrubs** 1–4 m tall; mature stems slender, glabrous; axillary buds with outer pair of

scales narrowly lanceolate, 2–5 mm long, long-acuminate, glabrous, appearing stipular. **Leaves** alternate to pseudo-opposite, with petioles 2–4 (6) mm long, slightly winged apically, glabrous; leaf blades coriaceous, ovate to lanceolate or elliptic, (3) 5–9 (11) cm long, (1.5) 3–5 (6.5) cm wide, base long-cuneate to rounded or sometimes short-attenuate, apex acute to acuminate, margin entire, slightly thickened, glabrous to moderately appressed glandular-fimbriate above and especially beneath, indistinctly 3–5 (7)-plinerved and also somewhat arcuately veined with inner lateral nerves arising ca. 1 cm from base, midrib thickened and raised in basal 1 cm then apically weakly impressed above, conspicuously raised beneath, lateral nerves plane to weakly impressed above and weakly raised beneath, reticulate nerves weakly raised but obscure on both surfaces. **Inflorescences** loose, umbelliform racemes; rachis glabrous to sparingly puberulent, 2–10 (20) mm long; floral bract persistent, ovate to lance-ovate or lanceolate, 1–3.3 mm long, glabrous to sparingly short-ciliate; pedicels thin, 10–20 (25) mm long, glabrous to sparsely puberulous, often glandular-fimbriate with trichomes 0.1–0.2 mm long at articulation; bracteoles persistent, medial, subopposite, ovate to lance-ovate, 1–3.2 mm long, glabrous to inconspicuously ciliate. **Flowers** 5-merous; calyx 4–7.8 mm long, glabrous, tube campanulate, 2–3 mm long, slightly papillose, base rounded, limb spreading-erect, 2–4.8 mm long, longer than the tube, commonly conspicuously striate (rarely smooth), lobes broadly triangular, 1.8–3.5 mm long, smooth, acute, sinuses acute; **corolla** aestivation valvate, fleshy, bistratose, broadly cylindric-campanulate, slightly narrowed toward base, widest at mouth, 7–10 mm long, 4–5 mm diam., externally glabrous to moderately appressed spiculate, internally densely floccose with a tangle of white, villous trichomes, pale greenish often suffused with red, lobes erect to spreading or reflexed, triangular, 2–2.2 mm long, acute, densely villous-floccose internally; **stamens** 10, ca. 5.2 mm long; filaments slightly adherent to base of corolla, ca. 3–3.2 mm long, ciliate at apical tips; connectives lacking spurs; anthers 3–3.5 mm long, thecae 2.2–2.5 mm long, strongly incurved at base, tubules distinct, ca. 1–1.2 mm long, glabrous, dehiscing by slightly introrse to perfectly terminal pores. **Berry** spherical, 8–10 mm diam., dark purplish.

*Vaccinium floccosum* is endemic to elfin and premontane cloud forests of eastern Costa Rica and western Panama, 1000–2500 m elevation. The species has been collected twice in Costa Rica (Limón Prov.: Caribbean slopes, Cantón Talamanca, Dto. Bratsi, Reserva Indígena Talamanca, Kivut, *J. Bittner 1494* and *G. Herrera 5191*). Flowering specimens have been collected in January–October; fruiting in May–December. **Rare/Infrequent.**

*Vaccinium floccosum* is characterized by its alternate to pseudo-opposite leaves with flat blades, entire margins and plinerved venation, conspicuously striate calyx limbs that are longer than the tubes, greenish corollas that are internally densely floccose apically, and anther tubules that are short,

ca. 1 mm long, glabrous, and dehiscence introrsely or by perfectly terminal pores. In Panama, leaf morphology is variable with populations from the Boquete region showing leaves pseudo-opposite, coriaceous and inconspicuously petiolate with blades ovate to ovate-lanceolate, apices acuminate, and bases rounded or short-attenuate, whereas populations from the Fortuna Dam area show leaves distinctly alternate, thinner coriaceous and more conspicuously petiolate with blades more lance-elliptic, apices longer acuminate, and bases tapering and cuneate. All leaf blades with rounded bases are also pseudo-opposite, whereas leaf blades with cuneate leaf bases may be either distinctly alternate or pseudo-opposite. The synonymy of *Vaccinium floccosum*, as listed above, indicates something of its anomalous characteristics. The relationships of this species are as close to the species centered about *V. poasanum* as they are to the largely West Indian species usually treated as *Symphysia racemosa* (Vahl) Stearn [= *Hornemannia racemosa* Vahl., but *V. racemosum* (Vahl) Wilbur & Luteyn]. The inclusion of all these species within *Vaccinium* does not significantly expand the limits of that extremely diverse genus and still seems to be the best treatment for the complex until a worldwide revision of the generic limits is undertaken. Vander Kloet (1985), whose study was based largely on the West Indian “*S. racemosa*,” argued against such an extension of the generic limits of *Vaccinium* claiming that such an expansion “is tantamount to making the genus a dumping ground for any Vaccinieae of uncertain affinity.” In Vander Kloet’s experience “the character unique to the genus “*Vaccinium*” is the absence of hypanthium enlargement prior to anthesis.” The species is visited by hummingbirds (Luteyn 3756).

***Vaccinium floribundum* Kunth in H.B.K., Nov. Gen. Sp. 3: 266, pl. 251. 1818. Illustrated: J. L. Luteyn, Fl. Ecuador 54: pl. 4. 1996. Figures 3 and 4.**

Terrestrial **shrubs** to dwarf, procumbent or scandent **subshrubs** 0.2–0.8 (1.2) m tall, sometimes arising from lignotubers to 10 cm diam.; mature stems terete, rugose, sometimes “warty” from swollen nodes of fallen leaves, glabrous; twigs subterete to angled, or bluntly angled, striate to ribbed, glabrous to densely short, white pilose or cinereous; axillary buds with outer pair of scales elliptic-ovate, ca. 1–2 mm long, apex acute or acuminate to rounded, glabrous to puberulent, inconspicuous not appearing stipular. **Leaves** with petioles subterete, flattened adaxially, 2–3 (4) mm long, short-pilose; leaf blades coriaceous, elliptic, ovate to ovate-lanceolate,

0.4–1.5 (2.5) cm long, 0.3–1.2 cm wide, base cuneate to rounded, sometimes short-attenuate, apex rounded to acute, margin minutely crenate-serrate with each tooth terminating in a short, glandular hair, glabrous to minutely puberulent above or along margins or midrib basally, usually minutely glandular-fimbriate beneath, midrib and other nerves and margins often lighter color beneath, pinnately nerved with 3–5 secondary nerves per side but these usually obscure, reticulate veinlets slightly raised on both surfaces or impressed above and raised beneath. **Inflorescences** racemose or rarely weakly paniculate, 6–10-flowered; rachis subterete, angled, striate, 1–2 (4.5) cm long, glabrous to puberulent; floral bract deciduous, membranous, broadly elliptic to ovate or oblong, 2.5–4.5 mm long, apex acute to rounded, margin usually curved inward, minutely appressed puberulent on abaxial surface to nearly glabrous, minutely ciliate and occasionally glandularly fimbriate apically; pedicels subterete, angled, striate, 3–4 (6) mm long, glabrous to short-pilose; bracteoles nearly basal, similar to floral bract, nearly half as long as pedicel at anthesis, 2.5–4.8 mm long. **Flowers** 4–5-merous (sometimes on same plant); calyx ca. 3–4 mm long, tube campanulate to short-cylindric, 1.5–1.8 mm long, glabrous to densely short-pilose, green to purplish, often heavily suffused with pink to red, limb erect-spreading, 0.8–1 mm long, smooth, glabrous, lobes triangular-ovate, acute or rarely obtuse, 1–1.5 mm long, glabrous, sinuses acute; **corolla** aestivation imbricate, membranous, unistratose, cylindric, 5–6.5 mm long, glabrous, white to pinkish, lobes ovate-oblong, ca. 1.5 mm long, obtuse; **stamens** 8 or 10, 3.8–6 mm long; filaments distinct, 2–2.5 mm long, densely short-pilose; connectives lacking spurs; anthers 2.5–3.5 mm long, thecae 1–1.5 mm long, tubules distinct, 1.5–2 mm long, glabrous, dehiscing by obliquely introrse pores; style about as long as corolla. **Berry** spherical, 4–6 mm diam., blue-black, glabrous, sometimes glaucous.

*Vaccinium floribundum* is distributed in high montane cloud forest, subpáramo thickets, and grass páramo, from Costa Rica to northern Argentina. In Costa Rica, it is rare and has been collected only at 2700–3740 m elevation in the Cordillera de Talamanca at Cerro Chirripó, the Sakira summit of the Buenavista massif, Cerro Sábila of the Cerro de la Muerte area, Cerro de las Vueltas, Cerro Echandi along the Costa Rica/Panama border, and Cerro Kamuk. In Costa Rica, flowering specimens have been collected in January, March, July, and August; fruiting collections in July–September and December. **Rare/Infrequent** (in Costa Rica and adjacent Panama).

*Vaccinium floribundum* is characterized by its small leaves the blades of which are pinnately nerved and minutely crenate-serrate margined, racemose inflorescences with small white to pink flowers, spurless connectives, and glaucous berries. In Costa Rica the stamens lack spurs, whereas populations in South America have at least vestigial spurs. *Vaccinium floribundum* is most close-

ly related to *V. consanguineum*, as mentioned above. The differences between *V. floribundum* and *Pernettya prostrata* are discussed with *Pernettya*.

**Vaccinium furfuraceum** Wilbur & Luteyn, *Sida* 21(3): 1609, fig. 2. 2005. Figure 8.

Much-branched, epiphytic **liana**; mature stems bluntly angled, densely canescent; axillary buds with outer pair of scales ovate, 0.7–1.2 mm long, short-acuminate, densely canescent, not appearing stipular. **Leaves** with petioles thin, ca. 2–3 mm long, 1–1.2 mm diam., spreading pilose; leaf blades coriaceous,  $\pm$  bullate, ovate, (2.5) 4–6 cm long, (1.2) 1.8–2.5 cm wide, base rounded, apex short-acuminate with the tip itself bluntly acute, margin entire, glabrous above or nearly so except midrib densely canescent at base becoming less dense to glabrate apically and moderately pilose along principal veins, moderately to densely spreading pilose to hirsute beneath along all nerves with hyaline trichomes up to 0.7 mm long, also with dense (especially noticeable when young), persistently short, thick (squamose), glandular fimbriae, ca. 0.1–0.2 mm long on both nerves and surfaces, weakly 5-plinerved with inner pair of lateral nerves arising ca. 0.8 cm above base, midrib and lateral nerves impressed above and raised beneath, reticulate veinlets raised on both surfaces. **Inflorescences** congested apically, sometimes appearing terminal,  $\pm$  short-racemose but with rachis often contracted and flowers appearing corymbose, 3–10 (12)-flowered, all parts (including calyx and corolla) densely and squamously glandular-fimbriate with appressed, tan, tawny to grayish, thickened trichomes 0.1–0.3 mm long, also sparingly to moderately short-pilose with hyaline spreading trichomes 0.3–0.6 mm long; rachis (2) 4–8 mm long; floral bract persistent, narrowly lanceolate to oblong-ovate, 2.5–2.6 mm long, ca. 1.2 mm wide, apex acute, glandular-fimbriate on lamina and at margin; pedicels cylindric, striate, (6) 10–19 mm long, extending to ca. 25 mm long after anthesis; bracteoles near base, lanceolate, ca. 2.8 mm long, 1.6 mm wide, apex long-acuminate, weakly ciliate, weakly glandular-fimbriate marginally. **Flowers** 5-merous; calyx 3–4.5 mm long, tube cylindric, ca. 1.5 mm long, base inconspicuously bluntly apophyseate, limb flaring or spreading, ca. 3 mm long, smooth, lobes broadly ovate, short-acuminate, ca. 1–1.2 mm long, tearing at sinuses with age, sinuses acute; **corolla** aestivation valvate, thin-carnose when fresh but membranous when dry, bistratose, cylindric-campanulate, broadening toward throat, 8–12 mm long, ca. 8 mm diam. across throat, brownish-lilac fide label (“café lila”), lobes ovate, 2.5–3 mm long, acute, glabrous within; **stamens** 10, 7–9.5 mm long; filaments distinct, 2–3 mm long, densely short-pilose in apical  $\frac{2}{3}$  especially at connective, conspicuously shorter than anthers; connectives lacking spurs; anthers ca. 7 mm long, thecae ca. 2–2.2 mm long, incurved and slightly apiculate at base, tubules distinct, 3–5 mm long, curving inward apically, short-pilose along inner surfaces near base, dehiscing by latrorse clefts ca. 1–2 mm long; style located to one side, slightly curved apically, slightly exserted; nectariferous disc cupular. **Berry** not seen.

*Vaccinium furfuraceum* is endemic to Costa Rica and is known only from the type collection from the southern slope of the Talamanca Valley, near the border with Panama (Limón: Cantón de Talamanca, between Río Sukut and Río Carbri, Muragubishi, 700 m, *G. Herrera 3286*). The type collection was flowering in July; fruits are unknown. **Endangered.**

*Vaccinium furfuraceum* is characterized by its generally densely glandular-fimbriate leaf blades and floral parts; thin-petiolate leaves with blades that are bullate, apically short-acuminate, and basally rounded; plinerved venation with the reticulate veinlets conspicuously raised beneath; short calyx lobes; thin and membranous corollas that are cylindric-campanulate; and staminal tubules that are pubescent along the inner surfaces and dehiscent laterally. The corollas are proportionally conspicuous with respect to the calyx. Its morphological relationships lie near *V. montevidense* and *V. jefense*, with which it has in common pilose inner surfaces of the staminal tubules and latrorse dehiscence. It also shares densely fimbriate leaves and inflorescence parts with *V. jefense*, perhaps its closest relative. *Vaccinium furfuraceum* differs most conspicuously from *V. jefense* by its possession of an overall shorter calyx (3–4.5 mm long vs. 6–10 mm) and calyx lobes (1–1.2 mm long vs. 4.5–6 mm), inconspicuously apophysate (not 10-ribbed) calyx tube, and nonstriate calyx limb and lobes.

***Vaccinium jefense*** Luteyn & Wilbur, *Brittonia* 29: 272. 1977. *Symphysia jefensis* (Luteyn & Wilbur) vander Kloet, *Taxon* 53: 97. 2004.

Epiphyte or arching terrestrial **shrubs**, sometimes lianoid to 2 m tall; mature stems subterete, glabrous; twigs subterete, glabrous to densely hirsute apically; axillary buds with outer pair of scales narrowly lanceolate, 2.5–6 mm long, long-acuminate, hirsute, appearing stipular. **Leaves** alternate, with petioles terete, rugose, 5–9 mm long, 2–3.5 mm diam., hirsute to glabrate; leaf blades coriaceous, elliptic or ovate-elliptic, (4.5) 8–12 (20) cm long, (2) 3–7 (8.5) cm wide, base rounded and cordate to subcordate, apex acuminate to short-acuminate, margin entire, glabrous above and sparsely to moderately hirsute beneath along principal veins, lower surface also bearing numerous, minute, glandular fimbriae, 5–7 (9)-plinerved (or sometimes weakly pinnately veined with 3 pairs of secondary nerves), midrib conspicuously thickened and raised in basal 1–2 (3) cm then apically impressed above and raised beneath, lateral nerves impressed above and raised beneath (i.e., leaves somewhat bullate), reticulate veinlets strongly impressed to slightly raised and conspicuous to more usually inconspicuous above but raised and conspicuous beneath. **Inflorescences** axillary, rarely appearing terminal, racemose,

sometimes appearing subcorymbose, (6) 8–17-flowered, sometimes 2–3 arising from same node; rachis subterete, 1–1.5 cm long, glabrous or sparsely hirsute, densely glandular-fimbriate; floral bract linear-lanceolate, (2.5) 3–9 mm long, ca. 1 mm wide, conspicuously nerved, hirsute, glandular-fimbriate; pedicels terete, striate, (6) 14–26 mm long, ca. 1 mm diam., sparsely hirsute, densely glandular-fimbriate; bracteoles linear-lanceolate, (2.5) 5–8 mm long, ca. 0.5 mm wide, hirsute, glandular-fimbriate. **Flowers** 5-merous; calyx 6–10 mm long, sparsely to moderately hirsute, sparsely to densely glandular-fimbriate, tube cylindric, conspicuously bluntly and roundedly 10-ribbed or fluted, 2–4 mm long, limb campanulate, 4–6 mm long, lobes oblong to ovate, conspicuously nerved, (2) 4.5–6 mm long, apex acute, often basally slightly imbricate, sinuses acute; **corolla** aestivation valvate, thin-carnose, weakly bistratose, cylindric-campanulate, 10–13.5 mm long, 5.5–10 mm diam., sparsely hirsute and glandular-fimbriate externally especially on lobes, green to pale translucent green, lobes triangular-deltate, 2–4 mm long and wide; **stamens** 10, ca. 8–10 mm long; filaments distinct, ca. 2.5–4 mm long, conspicuously broad at base, margin densely sericeous; connective lacking spurs, densely sericeous; anthers distinct, ca. 7–8 mm long, thecae ca. 3–3.7 mm long, strongly incurved at base, tubules distinct, ca. 3.5–5 mm long, longer than thecae, curved inward, sparsely long-pilose along inner surface, dehiscing by latrorse clefts ca. 1.5–2 mm long; style included, 9–10 mm long. **Berry** apparently spherical, ca. 12 mm diam, purple.

*Vaccinium jefense* is found in premontane and montane rain forest, elfin forest, and dense, moss-draped thickets, from western Chiriquí Province eastward through Panamá Province, Panama, (400) 750–1400 m elevation. It has not yet been collected in Costa Rica. Flowering specimens have been collected in January–July and sporadically throughout the rest of the year; fruiting collections throughout most of the year. **Rare/Infrequent** (in Panama).

*Vaccinium jefense* is characterized by its weakly bullate leaf blades that are basally rounded and subcordate to cordate, conspicuous leaf nervation, glandular-fimbriate (sometimes densely) inflorescences, long and narrow bracteoles, elongate and conspicuously striate calyx limb and lobes, sparsely hirsute corollas (especially on the lobes), and anther tubules that are sparsely long-pilose along the inner surfaces and dehisc by latrorse clefts. It resembles several other green-flowered species of *Vaccinium*, and its morphological relationships are mentioned above in the discussion of *V. furfuraceum*.

***Vaccinium luteynii*** Wilbur in Wilbur & Luteyn, *Sida* 21(3): 1611, fig. 3. 2005.

Terrestrial or epiphytic **shrubs** to 4 m tall; mature

stems terete, epidermis cracking longitudinally, glabrous; twigs subterete to complanate, striate, glabrous; axillary buds with outer pair of scales lanceolate, 2.4–3 mm long, long-acuminate, appearing stipular. **Leaves** subopposite, with petioles stout, 1–5 mm long, glabrous; leaf blades coriaceous, ovate to oblong-ovate or ovate-elliptic, ca. 5–15 cm long, 3–6 cm wide, base rounded to almost subclasping, apex acute to somewhat acuminate, margin entire, slightly thickened and revolute, glabrous or nearly so on both surfaces, 3–5 (7)-plinerved with lateral nerves arising from basal  $\frac{1}{4}$ – $\frac{1}{3}$  of midrib, midrib basally much thickened and weakly raised in proximal  $\frac{1}{4}$  abaxially, then thinner and weakly impressed becoming plane to slightly raised near apex, lateral nerves weakly impressed to plane basally abaxially but soon slightly raised apically, reticulate veinlets raised abaxially, all venation somewhat raised beneath. **Inflorescences** axillary (often appearing terminal), corymbose racemes, 10–13-flowered; rachis bluntly angled, 1.5–4.5 cm long, glabrous to sparingly and minutely puberulent; floral bract persistent, scale-like, triangular or lanceolate, 2–2.5 mm long, midrib prominent, glabrous but often minutely ciliate; pedicels irregularly angulate or ridged, 20–40 mm long, ca. 0.6–1 mm diam., glabrous; bracteoles persistent, basal, subopposite, lanceolate to narrowly triangular, 1.2–2 mm long, glabrous or minutely ciliate. **Flowers** 5-merous; calyx subglobose, 4–4.2 mm long, glabrous, tube subcylindric, deeply and bluntly rugose, ca. 1 mm long, limb ca. 3 mm long, smooth above but broadly and saccately spurred opposite and below each lobe, the spurs solid and sometimes slightly and broadly bilobed, calyx lobes triangular, 0.6–1 mm long, acute, glabrous; **corolla** aestivation valvate, thick and somewhat fleshy, bistratose, broadly urceolate to urceolate-campanulate, 5–8 mm long, ca. 6 mm diam. just beneath throat and 3.5–4 mm diam. at base (ca. 10 mm long and 8 mm broadest diam. when fresh), green, externally glabrous and internally densely pilose with whitish trichomes especially at throat and on lobes, lobes triangular, ca. 3 mm long, acute; **stamens** 10, shorter than corolla, ca. 6.5 mm long; filaments 3.5–4 mm long, long-pilose in apical  $\frac{1}{2}$ ; connectives lacking spurs; anthers ca. 3.5 mm long, thecae ca. 2–2.5 mm long, lower  $\frac{1}{3}$  strongly incurved upward, tubules distinct, stout, ca. 1 mm long, glabrous, dehiscing by introrse, strikingly oblique pores; style included. **Berry** not seen.

*Vaccinium luteynii* is endemic to the montane rain forest of western Panama, along the Continental Divide between Bocas del Toro and Chiriquí provinces, 700–950 m elevation. The species is to be expected in Costa Rica. Flowering specimens have been collected in March and October; fruits are unknown. **Endangered.**

*Vaccinium luteynii* is characterized by its subopposite leaves; glabrous leaf blades with rounded to almost subclasping bases; saccately 5-spurred calyx limb; thick, fleshy, broadly urceolate to urceolate-campanulate corollas that are internally densely pilose at the throat and onto the lobes; and glabrous stamens that dehiscence introrsely. The interspecific relationships of *V. luteynii* are uncertain

at this time, although it is morphologically similar to *V. bocatorensis* and *V. floccosum*.

***Vaccinium monteverdense*** Wilbur & Luteyn in Luteyn & Wilbur, Brittonia 53: 442, fig. 2. 2001.

Epiphytic, possibly rarely terrestrial **shrubs**; mature stems pendent, 1–2.5 m long, arising from a lignotuber, terete, somewhat rugose, blackish-brown; twigs subterete, striate, glabrous; axillary buds with outer pair of scales lanceolate, 1.5–3 mm long, apex acuminate, glabrous to short-pilose at tip only, sometimes ciliate, appearing stipular but not conspicuous. **Leaves** with petioles subterete, narrowly winged often over entire length, rugose, 4–8 mm long, glabrous; leaf blades thick-coriaceous, weakly bullate, noticeably concave, ovate-lanceolate, (2.4) 3.4–8 cm long, (0.8) 1.2–2 (2.7) cm wide, base rounded or obtuse, usually shortly attenuate and narrowly decurrent onto petiole for 2–3 mm, apex bluntly and somewhat abruptly acuminate to short-acuminate, margin entire, glabrous, base of lamina beneath with two circular, concave, blackish glands ca. 0.2 mm diam., one on either side of midrib, these sometimes each bearing the base of a single glandular trichome, 3 (5)-plinerved with usually only midrib prominent, midrib weakly impressed above and raised beneath, lateral nerves and reticulate veinlets generally obscure, usually plane to weakly impressed or weakly raised above (or inner pair of lateral nerves impressed and prominent in basal half) and weakly raised beneath. **Inflorescences** racemose, 7–9 (16)-flowered; rachis subterete to bluntly angled, striate, 2–3 (4.7) cm long, glabrous; floral bract minute, deciduous, ovate, 0.8–1.5 mm long, apex acuminate, glabrous; pedicels subterete, striate, 14–19 mm long, glabrous but surrounded by stout, blackish, glandular fimbriae at articulation; bracteoles basal, subopposite, similar to floral bract. **Flowers** 5-merous; calyx 10–16 mm long, glabrous, tube cylindric to obconical, 4.5–8.5 mm long, striate to slightly ribbed, limb spreading to campanulate, 5.5–7.5 mm long, conspicuously striate, lobes broadly ovate, acute, 2.5–3.5 mm long, apparently tearing with age and the margins callose-thickened, sinuses sharply acute; **corolla** aestivation valvate, thinly fleshy, bistratose, broadly cylindric-campanulate, 13–18 mm long, 9–15 mm diam. at throat, green suffused with maroon to reddish-maroon or purplish apically in throat and lobes, glabrous, lobes strongly reflexed, deltate, ca. 3–3.5 mm long, acute; **stamens** 10, appressed to corolla, ca. 11.5–12 mm long; filaments distinct although slightly adherent to base of corolla, ca. 4.7–5 mm long, marginally long-pilose; connectives lacking spurs; anthers ca. 8–8.4 mm long, thecae ca. 3.2–3.4 mm long, with a minute, blunt apiculus at base, tubules distinct, slightly spreading, ca. 4.8–5 mm long, long-pilose along inner surfaces, dehiscing by short, slightly latrorse clefts ca. 1.4–1.5 mm long; style about equaling corolla. **Berry** unknown, but immature fruit spherical and at least 8 mm diam. with the limb still conspicuous.

*Vaccinium monteverdense* is found in premontane cloud forest and lower montane wet forest, 790–1700 m elevation. It is endemic to the Cor-

dillera de Tilarán (Monteverde region, Puntarenas Prov.) of Costa Rica, where it has been collected 10 times. Flowering specimens have been collected in January–May and October; immature fruiting plants in May. **Endangered.**

*Vaccinium monteverdense* is characterized by having leaf blades with two circular, concave, blackish glands ca. 0.2 mm diam., one on either side of midrib on lower surface; conspicuously striate calyx limb; cylindric-campanulate corolla that is mostly green but suffused with maroon or reddish-maroon apically; stamens that are adherent to the base of the corolla; relatively long filaments; and anthers with pilose tubules that dehisce latrorsely. Furthermore, its leaves are often slightly bullate and concave. At Monteverde, *V. monteverdense* may be confused with *Gonocalyx costaricensis*, which grows in the same general area, because of its striate calyx limb, somewhat broad corolla, and similar leaves; but *G. costaricensis* normally has flat leaves that lack the circular basal glands, totally red corollas that are strictly cylindric and much thinner in texture, and stamens with thin, elongated tubules. The relationships of *V. monteverdense* are uncertain at this time.

***Vaccinium orosiense*** Wilbur & Luteyn in Luteyn & Wilbur, *Brittonia* 29: 275. 1977. *Symphysia orosiensis* (Wilbur & Luteyn) vander Kloet, *Taxon* 53: 97. 2004. Figure 6.

Terrestrial or epiphytic **shrubs** 1–2 m tall, sometimes scandent; mature stems terete to subterete, sometimes complanate, epidermis cracking longitudinally, glabrous; twigs subterete, striate, glabrous; axillary buds with outer pair of scales narrowly lanceolate, 2.5–3.5 mm long, abruptly long-acuminate, appearing stipular. **Leaves** appearing subopposite especially on young twigs, clasping to amplexicaul, subsessile with petioles ca. 1 mm long, glabrous; leaf blades coriaceous, ovate to ovate-lanceolate, (2) 4–9 (14) cm long, (1.5) 3–5 (7) cm wide, base rounded to cordate, apex acute, bluntly acute to shortly and bluntly acuminate, margin entire and slightly thickened, glabrous to sparsely and inconspicuously appressed, glandular-fimbriate, 5–7 (9)-plinerved with inner lateral nerves arising up to 3 cm above base, midrib thick and raised above in basal ½ then weakly raised to plane apically, conspicuously raised beneath, lateral nerves weakly raised on both surfaces but conspicuous beneath, reticulate veinlets weakly raised, conspicuous and of a slightly lighter color on both surfaces. **Inflorescences** umbelliform racemes, often superficially appearing terminal; rachis 1–1.5 cm long, glabrous; floral bract persistent, scale-like, triangular to ovate-lanceolate, 1–2.2 mm long, glabrous to minutely ciliate; pedicels 15–25 mm long, glabrous; bracteoles located along basal ¼ of pedicel, subopposite, appressed, persistent, deltate

to lance-ovate, 0.8–1.5 mm long, glabrous to inconspicuously ciliate. **Flowers** 5-merous; calyx 2–4 mm long, glabrous, tube campanulate to urceolate, 2–3 mm long, limb 0.5–1 mm long, smooth, lobes triangular, 0.5–1.2 mm long, acute; **corolla** aestivation valvate, fleshy, bistratose, cylindric to urceolate, 5–8 mm long, 5–7 mm diam., yellowish-green often suffused with maroon, externally glabrous but internally moderately to densely pilose with white trichomes in upper half and especially on lobes, lobes spreading or reflexed, triangular, 1–1.2 mm long, acute; **stamens** 10, ca. 6 mm long; filaments weakly adherent to base of corolla, ca. 3 mm long, villos; connectives lacking spurs; anthers ca. 4 mm long, thecae 1.5–2.3 mm long, incurved and apiculate at base, tubules distinct, 1.5–2 mm long, ca. 0.5 mm diam., glabrous, dehiscing by slightly introrse, oblique pores; style about equaling corolla. **Berry** spherical, ca. 12 mm diam., “morada” in color (fide label).

*Vaccinium orosiense* is found in premontane cloud forest, 1130–1800 m elevation. It is endemic to the Caribbean slope of Costa Rica (Cartago, Parque Nacional Tapantí) and adjacent western Panama (Chiriquí Prov., Fortuna Dam area). It is rare in Costa Rica and has been collected only six times. Flowering specimens have been collected in May and December–January; fruiting in January, June, and December. **Rare/Infrequent.**

*Vaccinium orosiense* is characterized by its amplexicaul leaves with rounded or cordate blade bases, short calyx lobes, corollas that are moderately to densely pilose internally at the throat, and short anther tubules. When fresh, the basal region of the leaf blades is red, as is also the case in *V. costaricense*, *V. floccosum*, and *V. luteynii* but usually not in *V. poasanum*. The relationships of *V. orosiense* are mentioned under the discussion of *V. costaricense*.

***Vaccinium poasanum*** J. D. Smith, *Bot. Gaz.* 24: 395. 1897. *Symphysia poasana* (J. D. Smith) vander Kloet, *Taxon* 53: 97. 2004. Figures 2X and 8.

Terrestrial or epiphytic **shrubs** or small **trees** (1) 2–5 (7) m tall; mature stems and twigs glabrous, bole (when present) up to 30 cm dbh; axillary buds with outer pair of scales narrowly lanceolate, (1.7) 2–4.8 mm long, abruptly long-acuminate, appearing stipular. **Leaves** with petioles 1–4 mm long, glabrous to hirsutulous; leaf blades coriaceous, ovate, lanceolate or elliptic to ± obovate, 3–8 (10) cm long, (1) 2.5–4 (6) cm wide, base acute to broadly cuneate, very rarely auriculate, apex acute to acuminate, margin entire, glabrous or rarely short-puberulent basally, sparingly to moderately appressed glandular-fimbriate above and especially beneath, indistinctly 3–5-plinerved and also somewhat arcuately veined, midrib thickened and slightly raised in the proximal 1 cm above and then plane to slightly impressed apically, lateral nerves weakly impressed above,



all nerves raised beneath but reticulate veinlets sometimes obscure. **Inflorescences** umbelliform racemes, (4) 7–13-flowered; rachis 0.5–2 cm long, glabrous to sparingly puberulent; floral bract persistent, lance-ovate to lanceolate, 1.5–2.5 mm long, ciliate; pedicels slender, 7–15 mm long, sparingly puberulent, often with glandular-fimbriate trichomes 0.1–0.2 mm long at articulation; bracteoles submedial, subopposite, lance-ovate to lanceolate, 1–1.5 mm long, ciliate, often persistent. **Flowers** 5-merous; calyx 3.5–5 mm long, glabrous to densely puberulent, tube short-campanulate to turbinate, 2–3.5 mm long and in diam., limb wide-spreading, 1–2 mm long, smooth, lobes broadly and shallowly deltate, 0.2–1 mm long, apiculate, sinuses concave or flat; **corolla** aestivation valvate, thinly fleshy, bistratose, broadly cylindric, 8–12 mm long, 6–10 mm diam., glabrous, pale yellowish or greenish-white and occasionally tinged with bright rose or pink, lobes erect to slightly recurved, broadly oblong, 2–3.5 mm long, acute to obtuse; **stamens** 10, 7.5–8.5 mm long; filaments distinct, 2–2.5 mm long, broadened at base, slightly adherent to base of corolla, ciliate, conspicuously shorter than anthers; connectives lacking spurs; anthers 6–7 mm long, thecae 1.8–2.2 mm long, incurved at base, tubules distinct, 3.5–5.5 mm long, glabrous, dehiscent by slightly introrse, oblique pores; style longer than corolla, slightly exserted. **Berry** subglobose, 7–10 mm diam., dark purple.

*Vaccinium poasanum* is found in montane cloud forest to subpáramo, (900) 1500–3000 m elevation. It is broadly distributed from Guatemala to Panama. In Costa Rica, it is common in the cordilleras Central, Talamanca, and Tilarán. Flowering specimens have been collected in December–July; fruiting in January–April and July–September. **Common.**

*Vaccinium poasanum* is characterized by its leaves with acute to broadly cuneate blade bases and acute to acuminate apices, apiculate calyx lobes, broadly cylindric corollas, staminal filaments that are conspicuously shorter than the overall anthers, and elongate anther tubules. Throughout the extensive range of this species (Guatemala to Panama), the shape of the leaf base is very stable, that is, narrowing and acute to broadly cuneate. Two recent collections, however, from the Cordillera Tilarán (Monteverde area), Luteyn *et al.* 15234 and 15409, have leaf bases that are auriculate; otherwise, the characters are those of *V. poasanum*. This extremely rare variant of leaf base shape, uncommon in Ericaceae as a whole, would, under normal circumstances, probably tempt us to recognize it formally were it not for the fact that it has also been noticed in two collections of *V. costaricense* from the Cordillera Central (mentioned above). Like many other of the green-flowered species of *Vaccinium*, the interspecific relationships of *V. poasanum* are uncertain. It is, however, morphologically similar to

another unpublished new species endemic to central Panama (Cerro Campana, Panamá Prov.) that differs by having shorter and narrower leaf blades ( $2\text{--}4.7 \times 1.2\text{--}2.4$  cm vs.  $3\text{--}10 \times [1] 2.5\text{--}6$  cm) with rounded bases (vs. bases acute, broadly cuneate or acuminate), 1–3-flowered racemes (vs. [4] 7–13-flowered), puberulous to short-pilose pedicels and rachises (vs. glabrous to sparingly puberulent), a cylindric calyx tube that is striate and bluntly 5–10-ribbed when fresh (vs. short-campanulate to turbinate, terete, and smooth), 4–5 mm long calyx lobes (vs. 0.2–1 mm long), anther thecae that nearly equal the anther tubules (vs. conspicuously shorter), and latrorse dehiscence by means of elongate clefts (not slightly introrse by oblique pores). *Vaccinium poasanum* is visited by the hummingbird *Selasphorus scintilla* in Costa Rica (pers. observ.; Luteyn, 1998).

***Vaccinium talamancense*** (Wilbur & Luteyn) Luteyn, Brittonia 53: 444. 2001. *Macleania talamancensis* Wilbur & Luteyn in Luteyn & Wilbur, Brittonia 29: 263, fig. 3. 1977.

Terrestrial **shrubs** 0.5–1 m tall, without lignotubers; mature stems terete, striate, glabrous; twigs subterete, bluntly and broadly complanate, glabrous or puberulent to densely short-pilose, glabrate; axillary buds with outer pair of scales lanceolate, ovate to broadly ovate, 3–6 mm long, up to 3 mm wide at base, long-acuminate, short-pilose or ciliate, appearing stipular but not conspicuous. **Leaves** imbricate, with petioles thick, rugose, 2–3 mm long, flattened or broadly canaliculate adaxially and slightly winged throughout, glabrous or moderately puberulous to short-pilose; leaf blades coriaceous, obovate to more typically oblong-elliptic, 2.5–4.7 cm long, 1.2–1.8 (2.3) cm wide, base rounded, apex acute or rounded but with a 1–3 mm long apiculus, margin indistinctly and minutely serrulate, margin a lighter color and seemingly thinner than lamina proper, essentially glabrous above except midrib finely whitish-appressed-pilosulous near base and margin inconspicuously ciliate especially basally, beneath indistinctly and sparingly whitish-appressed-pilosulous at base and also with 1–2 reddish, circular glands, entire surface beneath also bearing appressed, reddish-brown, glandular fimbriae ca. 0.2 mm long, pinnately nerved with 3–4 arcuate-ascending secondary nerves per side, midrib slightly thickened and raised basally but impressed apically, secondary nerves impressed above, all nerves prominent and raised beneath and of a lighter color than lamina proper. **Inflorescences** racemose, 10–15-flowered; rachis strongly and sharply angled, 1–2 (4) cm long, softly short, white pilose; floral bract appressed, linear to lanceolate, 3–4 mm long, puberulent; pedicels 6–10 mm long, softly pilosulous or puberulous, bearing a series of glandular fimbriae apically at articulation; bracteoles basal, appressed, linear to narrowly lanceolate, 2–3 mm long, puberulent, margin glandular-fimbriate. **Flowers** 5-merous; calyx 4.5–5 mm long, tube campanulate to cylindric, ca. 2.5–



3 mm long and diam., moderately puberulous with whitish trichomes ca. 0.1–0.2 mm long, limb slightly flaring to campanulate-spreading, 2–2.8 mm long, smooth, lobes triangular, 1.2–1.8 mm long, acute, puberulous externally and internally, sinuses concave; **corolla** aestivation apparently valvate, membranous (weakly membranous when fresh), cylindric, terete, 8–13 mm long, 4–6 mm diam., appressed- to spreading-puberulous externally with moderately abundant hyaline trichomes ca. 0.4 mm long, moderately to densely pilose with hyaline trichomes internally, pink to red although lobes sometimes pale pink to whitish, lobes strongly reflexed, triangular, 1.5–2 mm long, densely pilosulous both externally and internally; **stamens** 10, alternately slightly unequal, ca. 7–8.8 mm and 7.5 mm long; filaments distinct, alternately slightly unequal, ca. 3.5–4.7 and 4 mm long, glabrous basally but margin with appressed, short-pilose, hyaline trichomes apically, inconspicuously shorter than anthers; connectives lacking spurs; anthers 4.5–5.5 mm long, thecae 1.8–2.8 mm long, strongly incurved at base, tubules distinct, 2.5–3 mm long, glabrous, dehiscing by introrsely oblique pores ca. 0.6–1.4 mm long; style exserted. **Berry** spherical, 8–13 mm diam, short-pilose, blue-black.

*Vaccinium talamancense* is endemic to the *Quercus* forest and secondary, rocky scrub in the open páramo of Cerro Chirripó, 2590–3460 m elevation. Flowering plants have been collected in January–April; fruiting plants in March, September, and December. **Endangered**.

*Vaccinium talamancense* is characterized by its leaves with blade margins indistinctly and minutely serrulate, red to pink corollas that are appressed- to spreading-puberulous externally and moderately to densely pilose internally, anther connectives that lack spurs, and a pilose berry that is not glaucous. Its interspecific relationships are uncertain at this time. *Vaccinium talamancense* was originally described in *Macleania* by Wilbur and Luteyn (in Luteyn & Wilbur, 1977) but with more complete material and fieldwork was subsequently shown clearly to belong in *Vaccinium* (Luteyn, 2001). The species is visited by hummingbirds (pers. observ.).

## Literature Cited

- ANDERBERG, A. A. 1992. The circumscription of the Ericaceae and their cladistic relationships to other families of “higher” dicotyledons. *Systematic Botany*, **17**: 660–675.
- . 1993. Cladistic interrelationships and major clades of the Ericales. *Plant Systematics and Evolution*, **184**: 207–231.
- BIDARTONDO, M. I., AND T. D. BRUNS. 2001. Extreme specificity in epiparasitic Monotropoideae (Ericaceae): Widespread phylogenetic and geographical structure. *Molecular Ecology*, **10**: 2285–2295.
- BLAKE, S. F. 1915. A new *Vaccinium* from Costa Rica. *Journal of Botany*, **53**: 271–272.
- . 1922. New plants from South and Central America collected by Wilson Popenoe. *Proceedings of the Biological Society of Washington*, **35**: 117–124.
- CAMP, W. H. 1939. Studies in Ericales. IV. Notes on *Chimaphila*, *Gaultheria* and *Pernettya* in Mexico and adjacent regions. *Bulletin of the Torrey Botanical Club*, **66**: 7–28.
- CLEMANTS, S. E. 1994. (1103) Proposal to conserve 6182 *Bejaria* (Ericaceae) with a conserved spelling and type. *Taxon*, **43**: 473–476.
- . 1995. *Bejaria*, in Ericaceae—Part II. The superior-ovary genera (Monotropoideae, Pyroloideae, Rhododendroideae, and Vaccinioideae p.p.). *Flora Neotropica Monograph*, **66**: 1–560. [*Bejaria*, pp. 54–106]
- COLWELL, R. K. 1973. Competition and coexistence in a simple tropical community. *American Naturalist*, **107**: 737–760.
- . 1985. Stowaways on the hummingbird express. *Natural History*, **7/85**: 57–63.
- CRONQUIST, A. 1981. *An Integrated System of Classification of Flowering Plants*. Columbia University Press, New York, 1262 pp.
- DIGGS, G. M. 1995. *Comarostaphylis*, in Ericaceae—Part II. The superior-ovary genera (Monotropoideae, Pyroloideae, Rhododendroideae, and Vaccinioideae p.p.). *Flora Neotropica Monograph*, **66**: 1–560. [*Comarostaphylis*, pp. 146–193]
- DORR, L. J. 1995. Pyroloideae, in Ericaceae—Part II. The superior-ovary genera (Monotropoideae, Pyroloideae, Rhododendroideae, and Vaccinioideae p.p.). *Flora Neotropica Monograph*, **66**: 1–560. [*Chimaphila*, pp. 37–45]
- JUDD, W. S., AND K. A. KRON. 1993. Circumscription of Ericaceae (Ericales) as determined by preliminary cladistic analyses based on morphological, anatomical, and embryological features. *Brittonia*, **45**: 99–114.
- KNAPP, S. 2002. Assessing patterns of plant endemism in neotropical uplands. *Botanical Review*, **68**: 22–36.
- KRON, K. A. 1996. Phylogenetic relationships of Empetraceae, Epacridaceae, Ericaceae, Monotropaceae, Pyrolaceae: Evidence from nuclear ribosomal 18S sequence data. *Annals of Botany (London)*, **77**: 293–303.
- KRON, K. A., AND M. W. CHASE. 1993. Systematics of the Ericaceae, Empetraceae, Epacridaceae, and related taxa based upon *rbcL* sequence data. *Annals of the Missouri Botanical Garden*, **80**: 735–741.
- KRON, K. A., AND J. L. LUTEYN. 2005. Origins and biogeographic patterns in Ericaceae: New insights from recent phylogenetic analyses. *Biologiske Skrifter*, **55**: 479–500.
- KRON, K. A., W. S. JUDD, P. F. STEVENS, D. M. CRAYN, A. A. ANDERBERG, P. A. GADEK, C. J. QUINN, AND J. L. LUTEYN. 2002a. Phylogenetic classification of Ericaceae: Molecular and morphological evidence. *Botanical Review*, **68**: 335–424.
- KRON, K. A., E. A. POWELL, AND J. L. LUTEYN. 2002b.

- Phylogenetic relationships within the blueberry tribe (Vaccinieae, Ericaceae) based on sequence data from *matK* and nuclear ribosomal ITS regions, with comments on the placement of *Satyria*. *American Journal of Botany*, **89**: 327–336.
- LUTEYN, J. L. 1975. The genus *Cavendishia* (Vacciniaceae) in Costa Rica. *Brenesia*, **6**: 9–18.
- . 1976a. Notes on neotropical Vaccinieae (Ericaceae). I. *Gonocalyx*—A genus new to Central America. *Brittonia*, **28**: 37–41.
- . 1976b. Notes on neotropical Vaccinieae (Ericaceae). III. New and noteworthy species from Mexico and Central America. *Brittonia*, **28**: 400–406.
- . 1976c. A revision of the Mexican-Central American species of *Cavendishia* (Vacciniaceae). *Memoirs of the New York Botanical Garden*, **28**: 1–138.
- . 1983. Ericaceae—Part I. *Cavendishia*. *Flora Neotropica*, Monograph, **35**: 1–290.
- . 1987a. New species and notes on neotropical Ericaceae. *Opera Botanica a Societate Botanica Lundensi*, **92**: 109–130.
- . 1987b. *Orthaea* (Ericaceae-Vaccinieae): New species and redefinition of the genus. *Nordic Journal of Botany*, **7**: 31–37.
- . 1990. *Gonocalyx amplexicaulis* (Ericaceae): A new Panamanian blueberry. *Systematic Botany*, **15**: 745–747.
- . 1991a. Key to the subfamilies and genera of neotropical Ericaceae. *Nordic Journal of Botany*, **11**: 623–627.
- . 1991b. A synopsis of the genus *Didonia* (Ericaceae: Vaccinieae) with two new species. *Systematic Botany*, **16**: 587–597.
- , ED. 1995. Ericaceae—Part II. The superior-ovary genera (Monotropeoideae, Pyroloideae, Rhododendroideae, and Vaccinioideae p.p.). *Flora Neotropica*, Monograph, **66**: 1–560. [*Pernettya*, pp. 365–383; *Gaultheria*, pp. 384–488]
- . 1996a. Ericaceae. *Flora of Ecuador*, **54**: 1–404, I–VIII.
- . 1996b. New species, new records, and neotypification of some Mesoamerican Ericaceae. *Brittonia*, **48**: 241–249.
- . 1996c [1997]. Redefinition of the neotropical genus *Anthopterus* (Ericaceae: Vaccinieae), including one new species. *Brittonia*, **48**: 605–610.
- . 1997. A review of and taxonomic realignments within the neotropical genus *Macleania* (Ericaceae: Vaccinieae). *BiolLlania*, **6**: 455–465.
- . 1998. Neotropical blueberries: The plant family Ericaceae. <http://www.nybg.org/bot/res/lut2>.
- . 2001. Two new species and two new combinations in Mesoamerican Ericaceae. *Brittonia*, **53**: 437–446.
- . 2002. Diversity, adaptation, and endemism in neotropical Ericaceae: Biogeographical patterns in the Vaccinieae. *Botanical Review*, **68**: 55–87.
- LUTEYN, J. L., AND J. F. MORALES. 1996[1997]. Four new species of *Cavendishia* (Ericaceae: Vaccinieae) from Costa Rica. *Brittonia*, **48**: 514–519.
- LUTEYN, J. L., AND D. S. SYLVA S. 1999. “Murri” (Antioquia Department, Colombia): Hotspot for neotropical blueberries (Ericaceae: Vaccinieae). *Brittonia*, **51**: 280–302.
- LUTEYN, J. L., AND R. L. WILBUR. 1977. New genera and species of Ericaceae (Vaccinieae) from Costa Rica and Panama. *Brittonia*, **29**: 255–276.
- . 2002. Ericaceae. *Flora Nicaragua*, **1**: 822–831.
- LUTEYN, J. L., J. B. HARBORNE, AND C. A. WILLIAMS. 1980. A survey of the flavonoids and simple phenols in leaves of *Cavendishia* (Ericaceae). *Brittonia*, **32**: 1–16.
- MANSFELD, R., AND H. O. SLEUMER. 1935. Revision der Gattung *Befaria* Mutis. *Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem*, **12**: 235–276.
- MAST, R. B., J. V. RODRIGUEZ-MAECHA, R. A. MITTERMEIER, AND C. G. MITTERMEIER. 1999. Tropical Andes, pp. 68–82. In R. A. Mittermeier, R. A., P. Robles Gil, and C. G. Mittermeier, eds., *Hotspots: Earth's Biologically Richest and Most Endangered Terrestrial Ecoregions*. CEMEX & Conservation International, Mexico, 430 pp.
- MIDDLETON, D. J., AND C. C. WILCOCK. 1990. A critical examination of the status of *Pernettya* as a genus distinct from *Gaultheria*. *Edinburgh Journal of Botany*, **47**: 291–301.
- NASKRECKI, P., AND R. K. COLWELL. 1998. Systematics and host plant affiliations of hummingbird flower mites of the genera *Tropicoseius* Baker & Yunker and *Rhinoseius* Baker & Yunker (Acari: Mesostigmata: Ascidae). *Monographs Thomas Say Publications in Entomology*. Entomological Society of America, 185 pp.
- POWELL, E. A., AND K. A. KRON. 2001. An analysis of the phylogenetic relationships in the Wintergreen Group (*Diplycosia*, *Gaultheria*, *Pernettya*, *Tepuia*; Ericaceae). *Systematic Botany*, **26**: 808–817.
- . 2003. Molecular systematics of the northern Andean blueberries (Vaccinieae, Vaccinioideae, Ericaceae). *International Journal of Plant Sciences*, **164**: 987–995.
- RYDBERG, P. A. 1914. *Pyrolaceae*. *North American Flora*, **29**: 21–32.
- SLEUMER, H. O. 1936. Die Arten der Gattung *Vaccinium* in Zentral- und Südamerika. *Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem*, **13**: 111–140.
- . 1985. Taxonomy of the genus *Pernettya*. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie*, **105**: 449–480.
- SMITH, A. C. 1932. The American species of Thibaudiaeae. *Contributions from the United States National Herbarium*, **28**: 311–547, 19 pls.
- . 1933. The genera *Sphyraspermum* and *Disterigma*. *Brittonia*, **1**: 203–232.
- . 1941. Vacciniaceae. In Woodson, R. E., Jr., and R. W. Schery, *Contributions toward a Flora of Panama*. V. *Annals of the Missouri Botanical Garden*, **28**: 438–452.
- STANDLEY, P. C. 1920–1926. *Trees and shrubs of Mexico*. *Contributions from the United States National Herbarium*, **23**: 1–1721. [*Polycodium* and *Vaccinium* pp. 1101–1103]

- STANDLEY, P. C., AND L. O. WILLIAMS. 1996. Ericales. Fl. Guatemala, Fieldiana: Botany, **24**(pt. 8): 73–127.
- STEVENS, P. F. 1971. A classification of the Ericaceae: Subfamilies and tribes. Journal of the Linnean Society. Botany, **64**: 1–53.
- STEVENS, P. F., J. L. LUTEYN, E. G. H. OLIVER, T. L. BELL, E. A. BROWN, R. K. CROWDEN, A. S. GEORGE, G. J. JORDAN, P. LADD, K. LEMSON, C. B. MCLEAN, Y. MENADUE, J. S. PATE, H. M. STACE, AND C. M. WEILLER. 2004. Ericaceae, pp. 145–194. In K. Kubitski, ed., Families of Flowering Plants, vol. VI.
- TAKHTAJAN, A. 1980. Outline of the classification of flowering plants (Magnoliophyta). Botanical Review, **46**: 225–359.
- VANDER KLOET, S. P. 1985. On the generic status of *Symphysia*. Taxon, **34**: 440–447.
- VANDER KLOET, S. P., J. L. BALTZER, J. H. APPLEBY, R. C. EVANS, AND D. T. STEWART. 2004. A re-examination of the taxonomic boundaries of *Symphysia* (Ericaceae). Taxon, **53**: 91–98.
- WALLACE, G. D. 1995. Monotropoideae, in Ericaceae—Part II. The superior-ovary genera (Monotropoideae, Pyroloideae, Rhododendroideae, and Vaccinioideae p.p.). Flora Neotropica, Monograph, **66**: 1–560. [*Monotropa*, pp. 19–25]
- WILBUR, R. L. 1992. A synopsis of the genus *Disterigma* (Ericaceae: Vaccinieae) in Mexico and Central America with the description of two previously undescribed species. Bulletin of the Torrey Botanical Club, **119**: 280–288.
- WILBUR, R. L., AND J. L. LUTEYN. 1978. Ericaceae. Fl. Panama. Annals of the Missouri Botanical Garden, **65**: 27–144.
- . 1981. Additions to the Ericaceae of Panama. Annals of the Missouri Botanical Garden, **68**: 154–166.
- YEO, P. 1967. Notes on some species of *Macleania* (Ericaceae). Baileyana, **15**: 45–59.

# Index

The index includes all accepted scientific names (in Roman type), synonyms (*italics*), as well as common English names (Roman) and vernacular Spanish names (*italics*), and scientific terms (Roman) that may not be familiar to all and that have been defined in the text. Page numbers of illustrations are in **boldface**. The text does not include new names or combinations.

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*Macleania glabra*  
*Macleania insignis* 6, 10, 11  
var. *linearifolia*  
*Macleania irazuensis*  
*Macleania linearifolia*  
*Macleania megabracteolata*  
*Macleania nitida*  
*Macleania ovata*  
*Macleania pentaptera*  
*Macleania racemosa*  
*Macleania rupestris* 2, 4, 6, 14  
*Macleania subracemosa*  
*Macleania talamancensis*  
*Macleania turrialbana*  
*madroño*  
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*Monotropa coccinea*  
var. *mexicana*  
var. *nicaraguensis*  
Monotropa hypopitys  
Monotropa uniflora 4, 5, 19, 20  
var. *coccinea*  
*muelas*  
*muelita*  
Mycerinus

Orthaea 21, 25  
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Orthaea panamensis 2, 5  
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*Pernettya buxifolia*

*Pernettya ciliata*  
*Pernettya ciliaris*  
var. *alpina*  
*Pernettya coriacea*  
*Pernettya hirta*  
*Pernettya howellii*  
*Pernettya oerstediana*  
*Pernettya prostrata* 4, 5, 8, 20  
*Pernettya setigera*  
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Pinus  
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*Polyboea crassifolia* 30  
*Polyboea quereme*  
*Polyboea veraguensis*  
*Polyboea warszewiczii*  
*Proclesia warszewiczii* 30  
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*Psammisia alpicola*  
*Psammisia costaricensis*  
*Psammisia glabra*  
*Psammisia ramiflora* 4, 6, 17  
*Psammisia rupestris*  
*Psammisia symphytemona*  
*Psammisia albrichianna* 17  
*Psammisia williamsii* 17  
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Rhinoseius richardsoni  
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Rhododendron simsii 2, 20  
*Riedelia clonantha*  
*Riedelia panurensis*  
*Riedelia warszewiczii*  
Rumex  
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Satyria 2, 17, 21  
Satyria allenii  
*Satyria clonantha*  
*Satyria elongata*  
Satyria meiantha 19  
*Satyria ovata*  
Satyria panurensis 5, 19  
Satyria species "A" 2, 4  
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*Satyria triloba*  
Satyria ventricosa  
Satyria warszewiczii 4, 17  
Selasphorus scintilla  
Siphonandra  
*Socratesia melastomoides*  
*Sophoclesia cordifolia*  
var. *normalis*  
var. *oophylla*  
*Sophoclesia flaccida*  
*Sophoclesia major*  
Spherospermum 2, 7, 9, 11, 21  
Spherospermum buxifolium 7

*Sphyrospermum cordifolium* 6, 7, 9

*Sphyrospermum dissimile* 4, 7

*Sphyrospermum ellipticum* 4, 9, 11

*Sphyrospermum linearifolium*

*Sphyrospermum majus*

*Sphyrospermum standleyi* 9

*Symphysia*

*Symphysia costaricensis*

*Symphysia floccose*

*Symphysia jefensis*

*Symphysia orosiensis*

*Symphysia ovata*

*Symphysia poasana*

*Symphysia racemosa*

*Symphysia tubulifera*

theca (pl., -ae) 1

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*Themistoclesia alata*

*Themistoclesia costaricensis* 4, 9

*Themistoclesia horquetensis* 4

*Themistoclesia pentandra* 4, 6, 9, 21

*Themistoclesia pterocarpa*

*Themistoclesia revoluta* 23

*Themistoclesia smithiana* 6, 7

*Themistoclesia valerii*

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*Thibaudia albiflora*

*Thibaudia archeri*

*Thibaudia bracteata* 29

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*Thibaudia crassifolia* 30

*Thibaudia floribunda*

*Thibaudia laurifolia*

*Thibaudia panurensis*

*Thibaudia quereme*

*Thibaudia rupestris*

*Tropicoseius*

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Vaccinieae 1, 3, 25

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*Vaccinium bocatense*

*Vaccinium consanguineum* 4, 6, 8, 12

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*Vaccinium costaricense* 4, 10, 12

*Vaccinium dissimile*

*Vaccinium floccosum* 4

*Vaccinium floribundum* 2, 7, 8

*Vaccinium furfuraceum* 4, 12

*Vaccinium irazuense*

*Vaccinium jefense*

*Vaccinium luteynii*

*Vaccinium monteverdense*

*Vaccinium orosiense* 4, 10

*Vaccinium pachycardium*

*Vaccinium poasanum* 4, 6, 12

*Vaccinium santafeense*

*Vaccinium smithianum*

*Vaccinium talamancense*

*Vaccinium valerii*









Families of seed plants known or expected to occur in Costa Rica and adjacent areas numbered according to the sequence of Engler's *Syllabus der Pflanzenfamilien*, edition 11, reworked by L. Diels (1936).

1	Cycadaceae	70	Caryophyllaceae	138	Caryocaraceae
2	Taxaceae	71	Nymphaeaceae	139	Marcgraviaceae
3	Podocarpaceae	72	Ceratophyllaceae	140	Quinaceae
4	Araucariaceae	73	Ranunculaceae	141	Theaceae
5	Pinaceae	74	Berberidaceae	142	Guttiferae, incl. Hypericaceae
6	Cupressaceae	75	Menispermaceae	143	Elatinaceae
7	Gnetaceae	76	Magnoliaceae	144	Cistaceae
8	Typhaceae	77	Annonaceae	145	Bixaceae
9	Potamogetonaceae	78	Myristicaceae	146	Cochlospermaceae
10	Najadaeae	79	Monimiaceae	147	Violaceae
11	Alismataceae	80	Lauraceae	148	Flacourtiaceae
12	Butomaceae	81	Hernandiaceae	149	Turneraceae
13	Hydrocharitaceae	82	Papaveraceae, incl. Fumariaceae	150	Passifloraceae
14	Triuridaceae	83	Capparidaceae	151	Caricaceae
15	Gramineae	84	Cruciferae	152	Loasaceae
16	Cyperaceae	85	Tovariaceae	153	Begoniaceae
17	Palmae	86	Resedaceae	154	Cactaceae
18	Cyclanthaceae	87	Moringaceae	155	Thymelaeaceae
19	Araceae	88	Droseraceae	156	Elaeagnaceae
20	Lemnaceae	89	Crassulaceae	157	Lythraceae
21	Mayacaceae	90	Saxifragaceae	158	Punicaceae
22	Xyridaceae	91	Brunelliaceae	159	Lecythidaceae
23	Eriocaulaceae	92	Cunoniaceae	160	Rhizophoraceae
24	Bromeliaceae	93	Hamamelidaceae	161	Combretaceae
25	Commelinaceae	94	Rosaceae	162	Myrtaceae
26	Pontederiaceae	95	Connaraceae	163	Melastomataceae
27	Juncaceae	96	Leguminosae	164	Onagraceae
28	Liliaceae	97	Krameriaceae	165	Halorrhagaceae
29	Haemodoraceae	98	Oxalidaceae	166	Araliaceae
30	Amarylloidaceae	99	Geraniaceae	167	Umbelliferae
31	Velloziaceae	100	Tropaeolaceae	168	Cornaceae
32	Dioscoreaceae	101	Linaceae, incl. Humiriaceae	169	Clethraceae
33	Iridaceae	102	Erythroxylaceae	170	Monotropaceae
34	Musaceae	103	Zygophyllaceae	171	Pyrrolaceae
35	Zingiberaceae	104	Rutaceae	172	Ericaceae
36	Cannaceae	105	Simarubaceae	173	Theophrastaceae
37	Marantaceae	106	Burseraceae	174	Myrsinaceae
38	Burmanniaceae	107	Meliaceae	175	Primulaceae
39	Orchidaceae	108	Malpighiaceae	176	Plumbaginaceae
40	Casuarinaceae	109	Trigonaceae	177	Sapotaceae
41	Piperaceae	110	Vochysiaceae	178	Ebenaceae
42	Chloranthaceae	111	Polygalaceae	179	Symplocaceae
43	Lacistemaceae	112	Dichapetalaceae	180	Styracaceae
44	Salicaceae	113	Euphorbiaceae	181	Oleaceae
45	Garryaceae	114	Callitrichaceae	182	Loganiaceae
46	Myricaceae	115	Buxaceae	183	Gentianaceae
47	Juglandaceae	116	Coriariaceae	184	Apocynaceae
48	Batidaceae	117	Anacardiaceae	185	Asclepiadaceae
49	Betulaceae	118	Cyrillaceae	186	Convolvulaceae
50	Fagaceae	119	Aquifoliaceae	187	Polemoniaceae
51	Ulmaceae	120	Celastraceae	188	Hydrophyllaceae
52	Moraceae	121	Hippocrateaceae	189	Boraginaceae
53	Urtiaceae	122	Staphyleaceae	190	Verbenaceae
54	Podostemonaceae	123	Icacinaceae	191	Labiatae
55	Proteaceae	124	Hippocastanaceae	192	Solanaceae
56	Oleaceae	125	Sapindaceae	193	Scrophulariaceae
57	Opiliaceae	126	Sabiaceae	193a	Schlegeliaceae
58	Loranthaceae	127	Balsaminaceae	194	Bignoniaceae
59	Aristolochiaceae	128	Rhamnaceae	195	Pedaliaceae
60a	Hydnoraceae	129	Vitaceae	196	Martyniaceae
60b	Rafflesiaceae	130	Elaeocarpaceae	197	Orobanchaceae
61	Balanophoraceae	131	Tiliaceae	198	Gesneriaceae
62	Polygonaceae	132	Malvaceae	199	Lentibulariaceae
63	Chenopodiaceae	133	Bombacaceae	200	Acanthaceae
64	Amaranthaceae	134	Sterculiaceae	201	Plantaginaceae
65	Nyctaginaceae	135	Dilleniaceae	202	Rubiaceae
66	Phytolaceae	136	Actinidiaceae	203	Caprifoliaceae
67	Aizoaceae	137	Ochnaceae	204	Valerianaceae
68	Portulacaceae			205	Dipsacaceae
69	Basellaceae			206	Cucurbitaceae
				207	Campanulaceae
				208	Compositae

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